

Invited Paper

The Phylogeny of Butterflies (Papilionoidea and Hesperioidea)

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Abstract. A phylogenetic tree for butterflies and skippers is derived, using the common possession of derived traits to delimit monophyletic taxa. All available characters of larvae, pupae, adults, and behavior are used, including various new characters. The traits of the progenitor are deduced, and the exact character changes at each point of the tree are specified. The tree accepted is mostly similar to that of Ehrlich. However, within Nymphalidae, Apaturinae is elevated to a subfamily distinct from Charaxinae; and within Lycaenidae, Curetinae is elevated to a subfamily branching from the base of the Riodininae line, and Aphnaeini is elevated to tribal status; Megathyminae clearly belongs to the monocotyledon-feeding branch of Hesperioidea. Most characters support the origin of Pieridae from the Papilionid ancestral line, and the origin of Lycaenidae from the Nymphalid-Libytheid ancestral line. The few characters that seem to have been subject to state reversal, or evolved the same state independently repeatedly, are discussed.

Introduction

This paper attempts to reconstruct the phylogenetic tree for butterflies. The major recent contributor to this subject was Paul R. Ehrlich, who published an intuitive tree based mainly on adult skeletal features (Ehrlich, 1958b) and a computer-analyzed tree based on similarity of various internal and external features of adults (Ehrlich, 1967). Many other authors have contributed studies of various aspects of the subject. Kristensen (1976) published a useful paper using the methods of cladistics, and presented a phylogenetic tree differing in significant features from those of Ehrlich. This paper compiles the available characters from the literature, and interprets them using phylogenetic (cladistic) methods. It includes various new characters, and other characters elucidated by systematically examining all butterfly families for characters previously reported for only one or a few taxa. I also made a special study of first-stage larvae (mainly using chaetotaxy, which will be reported elsewhere in detail) and have included characters of larvae and pupae and behavior which other authors have not used. Questionable characters

were examined (some were found to be useless, see Useless Characters, below).

The phylogenetic (cladistic) principles used are: 1) taxa above the species-level should be defined on the basis of the common possession of unusual derived traits; and 2) each named taxon should have only one root (the taxon should be monophyletic).

The first principle, called by cladists "synapomorphy", or the shared possession of derived ("apomorph") traits, has been used by a few good systematists for centuries. For example, the possession of a larval osmeterium, a unique derived trait, indicates that the family Papilionidae is monophyletic. The presence of special lobes on the prolegs, and of peculiar ant-related glands on larvae of Lycaenidae, suggests the monophyletic nature of taxon Lycaenidae (including Riodininae). Likewise, the common possession of the unique trait of "hindwing rubbing" is enough to set the Theclini-Lycaenini-Polyommardini apart from the rest of the Lycaeninae (though a reviewer states that *Charaxes*, a Charaxine Nymphalid, does this also to draw attention to a false head), while the possession of special lobelike abdomen glands on females of Pierinae-Coliadinae and a special posture for the wafting of the male-repellent scent produced, suggests that this group is a monophyletic entity. In practice, "derived" merely means that the character changed in state, thus in practice various trial trees are drawn with all the character changes placed at their proper points on each tree as indicated by the data, and that tree chosen which minimizes the number of character changes and minimizes the number of absurdities. However, characters that are unique, complex, and highly unusual, such as the evolution of an osmeterium, should be given more weight than common character changes or the mere loss of a structure.

The second principle is more controversial, but I think is gaining acceptance. For instance, it requires the division of the old class Reptilia, because the bird and mammal classes evolved from that omnibus class, making it not monophyletic unless birds and mammals are included in it too. I use these cladistic principles because they seem to be logical, and because Kristensen (1976) claims that cladistics supports a different classification than that of Ehrlich (1958b, 1967). My results, using a larger data set than that of Kristensen, but analyzed with the same principles, are more like those of Ehrlich (1958b), with a few changes in Lycaenidae and Nymphalidae. The trees adopted through intuition and computer-analyzed similarity by Ehrlich do not contradict the present tree.

Fossil Record

The first proto-butterfly apparently evolved in the Cretaceous perhaps 100-80 million years ago (mya), judging from the widespread distribution of the families

and subfamilies (except those with only a few species) in relation to continental drift (South America last touched Africa about 80 mya, Smith et al., 1981), and based on their relationships with flowering plants, which evolved mostly in the Cretaceous. However, butterflies could have evolved somewhat later, perhaps even in the Paleocene, as a few wind-blown adults and various extinctions could have confused the zoogeographic picture; but this is not as likely. The most "primitive" Hesperidae (many Pyrginae), Papilionidae (Baroniinae), Pieridae (Dis-morphiinae plus many Coliadinae), and many Lycaenidae, all feed on Leguminosae, so it is reasonable to assume that the proto-butterfly ate this family. Since the Leguminosae is one of the most "advanced" (derived) families of plants, the ancestral butterfly apparently evolved when the dicotyledons were rather far along in their evolution. However, many fossils of many diverse groups of Leguminosae are known from the early Cretaceous, which is consistent with 100 mya or older. There is uncertainty in time of butterfly origin because, by the time of the first known fossil butterflies, the families were apparently fully evolved. Eocene fossils (48 mya) include several Papilionidae (one like modern *Baronia*, Baroniinae), one Nymphalid (Satyrinae), and one Lycaenid (Riodininae) (Durden & Rose, 1978). Lower Oligocene fossils (38 mya) include Papilionidae, Pieridae, Nymphalidae (Satyrinae, Apaturinae close to modern *Doxocopa*, Nymphalinae close to modern *Hypanartia* and others), Libytheidae (close to modern *Libythea*), Lycaenidae, and Hesperidae (Scudder, 1889; Brown, 1976; Shields, 1976).

Source of Data

Many of the data are from Ehrlich (1958a, 1958b, 1960, 1961; Ehrlich and Davidson, 1961; Ehrlich and Ehrlich, 1962, 1963), but Kristensen (1976) gives other traits, Brock (1971) a few thorax characters, Petersen (1965) and Fracker (1915) some larval characters, and Mosher (1916) some pupal traits (but see Useless Characters, below). Munroe (1961), Klots (1931), and Eliot (1973) provide useful characters on several families. Other authors provide a few useful traits, as cited below. I have found characters on larvae (especially first-stage larvae—see Hinton, 1946 for terminology—and the larval Lycaenid head), on pupae, the adult wing base, thorax, legs, abdomen base, genitalia, and some characters of larval and adult behavior. A few of the characters have been reinterpreted as noted. Figures 1-2 illustrate structures on the thorax and wing base, because some new characters and names introduced by Brock (1971), Matsuda (1970), and Sharplin (1963a, 1963b) create some confusion that needs clarification by figures. Tables 1 and 2 list the complex characters. To chart the changes of a structure, note its state in "Traits of the Ancestor of Hesperioidea and Papilionoidea" below; then note that the structure retains this state in all taxa unless a change is stated later in the text. Of course, the original references, especially those of Ehrlich, should be consulted for a character also.

Character Enumeration

No phylogenetic tree can be acceptable unless accompanied by precise statements of exactly how each character changed at each point of the tree, documenting the transformation of the ancestral species into the living taxa. Cladistics has been criticized as being merely a classification of characters, but actually the precise listing of character changes at each point of the tree is one of its

strengths. The following is a reconstruction of the ancestor of butterflies and skippers, a justification for the branching sequence, and a listing of how each character changed at each point of the tree of Figure 3 during the evolution of butterfly families, subfamilies, and tribes.

The Moth Progenitor

The closest living relatives of the butterflies and skippers are the other Macrolepidoptera, namely the Sphingoidea, Bombycoidea, Noctuoidea, and Geometroidea (Scott, 1985), rather than the Butterfly Moths, Castniidae. The colorful non-folding wings of Castniidae are evidently a convergent adaptation to diurnal flight. The lack of a jugal fold in Castniidae is because this structure is involved in wing-folding (Sharplin, 1963-64). The Castniid antenna club is shaped like that of skippers, but Jacqueline Miller (pers. comm.) has found that the microscopic details of the antennae are totally different (the Castniid club also has a hairy tip). The paracoxal and marginopleural sulci (Fig. 1) are joined in some Castniidae as in Hesperidae (Brock, 1971), but their different arrangement in other Castniidae suggests convergence. Likewise the dorsal chamber of the heart of some Cossidae, as in butterflies (Hessel, 1969), has been interpreted as a phylogenetic link, but other Cossids have a looped heart or ventral heart like most primitive Ditrysia, which again indicates convergence, especially as other primitive ditrysians have evolved a looped heart. Miller (1971) found a wide orbit ("eye ring") in Castniidae, nearly as wide as that of skippers, but in skippers this structure is perhaps unique in having tiny ommatidia (Ehrlich, 1960), whereas my examinations show no ommatidia in the orbit of Castniidae, which is similar to that of other moths. Castniidae also share with Megathyminae (Hesperidae) larvae which bore into monocotyledons; however this must be convergence, because young *Megathymus* larvae make silked-leaf nests as do other skippers. First-stage Megathyminae larvae share many derived traits with Hesperinae, notably a lack of the second SD seta on thorax segments 2-3 of first instars.

Traits of the Ancestor of Hesperioidea and Papilionoidea

This ancestor had a large non-foldable hindwing, and apparently lost the spine (frenulum) and catch (retinaculum) that hook moth wings together. Only *Euschemon* (Hesperidae, Pyrginae) has a frenulum and retinaculum today. This trait needs discussion because it does not seem to obey any usual evolutionary principle. If we assume that, once lost, these parts cannot be regained, then, because *Euschemon* is otherwise a normal member of the Pyrginae (Evans, 1949), these parts must have been lost independently at least four and up to a dozen or more times (by the Hesperinae-Megathyminae ancestor, by the ancestor of Pyrrhopyginae, by the remaining Pyrginae, and by the ancestor of Papilionoidea). A more likely explanation is that a regulatory gene controlling the development of the frenulum and retinaculum lost its function through a mutation in the ancestor of all butterflies and skippers, and that after *Euschemon* evolved, a reverse mutation restored the function of the gene, activating the dormant frenulum-retinaculum genes. (A virus-transferred gene could have had the same result.) Forbes (1960) suggests that a tuft of setae at the end of a short thickening of the costa in Riodininae replaces a frenulum, perhaps a less-perfect reappearance of a similar origin.

Table 1. Character states among the families. a = absent; p = present; s = present but small; l = large; capitalized letters are derived states, uncapitalized letters are primitive stages; Macro = Macrolepidoptera.

Character	Pap	Pier	Nym	Lib	Lyc	Hesp	Macro
1st stage larval annuli	a	a	a	a	P	P	a
#L setae 1st stage prothorax	2	1(2)	2	2	2	2	2
ventral neck gland larva	A	pA	pA	pA	A	pA	aP
osmeterium	P	a	a	a	a	a	a
crochets in circle mature larva	a(P)	a	a	a(S)	a	P	a
lateral crochets mature larva	A(S)	A	A	S	A(S)	p	p
pupa attached by cremaster	p	p	p	p	pA	p	p
pupa attached by silk girdle	p	p	A	A	p(A)	p	?
temporal cleavage line pupa	A	A	A	A	A	p	p
antenna hooked	A	A	A	A	A	p	ap
antenna cleaning (e=epiphysis, F=femur tuft, T=tibia brush	e	A	FT	FT	FT	e	e
tiny ommatidia in eye orbit	a	a	a	a	a	P	a
retina cells cross (x) or rosette (r) shaped	x	x	r	r	r	?	?
fw R veins branched	P	P	P	P	PA	a	ap
fw vein 2A joins 1A	A	p	p	p	p	p	p
2nd median plate fw base	A	p	p	p	p	p	p
male forelegs	l	l	S	P	S(L)	l	l
pulvilli (f=forked; s=single)	A	S(A)	f(A)	f	S	f	f
tiny dorsal tarsal spines	P	P	a(P)	a	a(P)	a	a
spurs middle leg tibia	A	p	p	p	p	A	p
upper pair spurs hindleg tibia	A	A	A	A	A	p	p
antenna cleaning by foreleg (f) or middle leg (m)	f	f	M	M?	M	f	f
cervical sclerites united	P	a	a	a	a	a	a
prothorax presternum	A	A	p	p	p	p	p
anterior rim T1 spiracle adult	S	S	S	S	S	p	p
paracoxal sulcus joins marginopleural	P	P	P	P	P	a	a
meral sulcus metathorax	P	a	a	a	a	a	a
scutum 3 view from rear	S	S	L	L	L	p	p
prespiracular bar	p	A	p	p	p	p	p
postspiracular bar	a	P	aP	L	a	aP	a
horizontal chamber aorta	A	p	p	p	p	p	p
secondary sternopleural sulcus	A	A	L	S	L	S	a

Table 2. Character states among the subfamilies. Symbols are the same as in Table 1.

	Papil	Parn	Baron	Pseud	Dism	Col	Pier	Dan	Ithom	Satyr	Morph	Char	Apat	Nymph	Acræa	Calin	Libyth	Styræ	Rhod	Curet	Lycæ	Mega	Hesp	Trap	Pyrgæ	Coel	Pyrrh	Macro
secondary setae 1st instar	P	P	P	P	P	P	P	P	P	P	P	P	P	P	P	P	P	P	P	P	P	P	P	P	P	P	P	P
#SD setae on mesothorax 1st instar	5	4	6	—	1	2	2	2	—	2,1	2	2	2	2	2,5	2	—	1	—	3	7	0-3	1	1	—	2	—	2
#SD setae on mesothorax 1st instar	5	4	6	—	1	1	1	2	—	2,1	2	2	2	2	2,5	2	—	1	—	3	8	0-3	1	1	—	2	—	2
larval body scoli	aP	a	a	a	a	a	a	a	a	a	a	a	a	P	P	a	a	a	aP	a	a	a	a	a	a	a	a	aP
pupal middle leg touches eye	a	a	a	a	a	a	a	P	P	P	P	P	P	P	P	P	P	a	a	P	a	a	a	a	a	a	a	a
antenna scaled	p	pA	A	p	p	d	p	A	p	p	p	p	p	p	p	p	p	p	p	p	p	p	p	p	p	p	p	p
hw vein 3A	A	A	p	p	p	p	p	p	p	p	p	p	p	p	p	p	p	p	p	p	p	p	p	p	p	p	p	p
patagia	S	S	S	A	A	p	A	l	l	l	l	l	l	l	l	l	S	A	A	A	A	l	l	l	l	l	l	l
parapatagia	A	A	A	A	A	A	A	A	A	A	A	S	A	AS	A	A	A	A	A	A	A	l	l	l	l	l	l	l
anepisternum mesothorax	lS	lS	l	A	A	A	A	A	A	S	l	l	A	A	A	A	l	A	l	l	l	AS	l	l	l	l	l	l
mesodiscimen curved down to base of furca (a), partly curved (s), or extending straight back to furca (l)	L	L	S	L	L	L	L	L	L	L	L	L	L	L	L	L	L	A	A	A	A	A	a	a	a	a	a	a
adult peritrophic membrane from front of midgut (f) or delaminated from midgut epithelium (e)	f	—	—	—	—	f	f	f	—	e	—	e	—	e	—	—	—	—	—	—	f	—	e	e	e	—	—	f

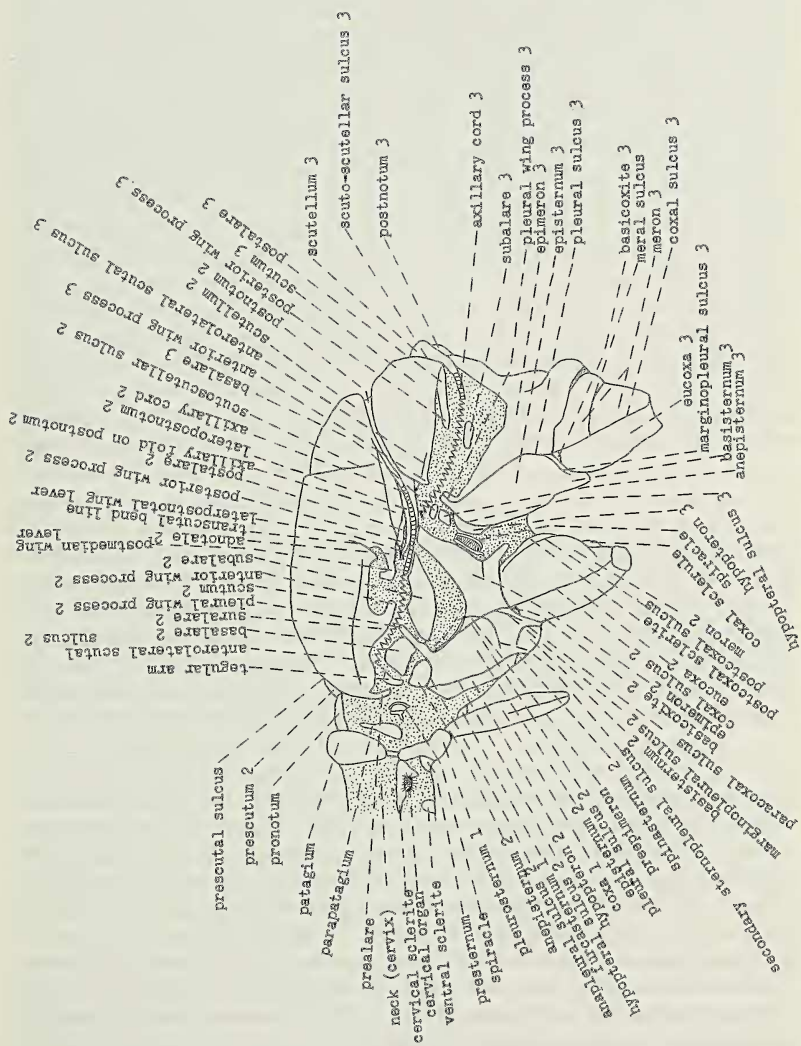


Fig. 1. Adult thorax, lateral view. Some terms in Figs. 1-2 differ from those of other authors, due to the work of Matsuda (1970), Sharplin (1963a, 1963b), and Brock (1971). When no clear-cut choice of terms was found, those of Matsuda were used, because his book covers all insects.

The wing veins of the ancestor resembled those of modern skippers (with no areole), except the hindwing discal cell was closed by a vein at its end, and hw vein M_2 was present. In the pupal forewing, R_{4+5} branched from the radius basad of R_1 and R_{2+3} (Headlee, 1907; Zeuner, 1943; Tindale, 1980). The ability to roof the wings over the abdomen was lost. Wing base structures were like those of other Macrolepidoptera such as Noctuidae (Sharplin, 1964). The antennae were clubbed, probably as in modern Papilionidae and Lycaenidae, or, farther back in time, as in some Sphingidae. The head lacked the two dorsal ocelli of most moths, but possessed chaetosemata. Adults were day fliers, and had large optic lobes of the brain for better vision. The head had paratemporal sulci (the temporal sulci of Miller, 1971) which are relatively unchanged in Hesperiiidae and Papilionoidea. The temporal cleavage line of the pupa ("epicranial suture" of Mosher, 1916) was present, and is represented in adults by the "transverse suture" of Miller (1971), which I am calling the temporal sulcus. The temporal sulcus of adult Papilionoidea (Ehrlich, 1958a) is probably homologous with Miller's "transverse suture" in Hesperiiidae, and has assumed a different course (parallel to the paratemporal sulcus) because the Papilionoid pupa lacks a temporal cleavage line (the position of the temporal sulcus in adult *Lycaena*, see Ehrlich 1958b, is perhaps primitive). The head had a distal transoccipital band and the laterofacial sulcus was lateral to the tentorial pits, as in Hesperiiidae (Miller, 1971). The foreleg had an epiphysis but no tibial spurs, the middle legs had two spurs, the hindlegs four. The pulvilli on the legs were forked; tiny dorsal spines were absent on the tarsi, but hairlike bristles were present above the claws. The aorta had an enlarged horizontal chamber with two lateral ostia in the mesothorax. The midgut was probably shaped like that of Hesperiiidae (Homma, 1954). On the thorax the presternum was present, the patagia and parapatagia were sclerotized, the first spiracle had a strong rim all around it, the paracoxal ("precoxal" of Brock, 1971) sulcus was not membranous and was directed anteriorly and not fused with the marginopleural sulcus, on the mesothorax the hypopteral sulcus (derived partly from the parepisternal sulcus of Brock, 1971) completely circled a hypopteron, the upper sector of the paracoxal sulcus (precoxal sulcus of Brock, 1971; see origin of Pieridae below) was lost, the secondary sternopleural sulcus developed, the anapleural cleft was fused together, and a postcoxal sclerite was on the top rear of the mesothorax meron. A muscle from the mesoscutellum to the mesopostnotum (pterothorax character #7 of Ehrlich and Ehrlich, 1963) was twisted, which Kristensen (1976) states is a derived feature of skippers and butterflies (except Lycaenids now have the muscle untwisted). Scutum 3 was visible somewhat from the rear, and a muscle from scutum 3 to the third phragma (pterothorax character #13 of Ehrlich and Ehrlich, 1963) was fan-shaped. The mesothorax discripen curved down to the furca base as in the metathorax, and the secondary furca arms in the metathorax were fused together for a short distance. The peritrophic membrane was apparently formed at the front of the adult midgut (Waterhouse, 1953). The transphragma between thorax and abdomen had two internal laminae (Brock, 1971). The anterolateral apodemes on the first abdomen sternite (sternum 2) became very small (tiny but present in all six families), a unique trait among Ditrysian Lepidoptera (except for some Limacodidae, Brock, 1971). Sternum 2 on the abdomen had a long anterolateral projection to the thorax and tergum 1 (the prespiracular bar). (Another character, the postspiracular bar, was possibly present also, but is functionally related to the

prespiracular bar, so if one is present the other is usually absent. It is complete only in Pieridae, a few Nymphalidae, Libytheidae, and a few Hesperidae such as *Capila* but not *Epargyreus*.) The pupa had clubbed antennae, and a temporal cleavage line between antenna bases ("epicranial suture" of Mosher, 1916), maxillary palpi were absent, the mandible remnants ("pilifers" of Mosher, 1916) were usually close together or touching, the femur was not visible on the foreleg, and the abdomen had only weak setae (no spines) and was movable only at joints 4-5, 5-6, and 6-7. The pupa lacked a silk cocoon, and was attached by both the cremaster and a silk girdle. The larvae ate leaves of dicotyledon plants, probably Leguminosae. Mature larvae had hundreds of short secondary setae, and the crochets were in three lengths (triordinal), in one row (uniserial), in a circle or (probably) inner semicircle. But first stage larvae had only "primary setae" (see Hinton, 1946 for names of these), including one SV and two SD setae on the meso- and metathorax, one L seta on abdomen segment 9, setae L1 and L2 were far apart on abdomen segments 1-8, and the crochets were probably in a circle. The postnatal ("subprimary") seta L3 was absent on the prothorax of second-stage larvae (secondary setae obscure its absence in older larvae). Proprioceptor seta MXD1 may have been absent on the prothorax, as it is absent in the few living taxa checked (*Pieris*, Hinton, 1946; apparently *Everes*, and *Lycaena*, Wright, 1983). The older larva had a ventral neck gland, now present in Hesperidae (Hesperinae at least), Pieridae (Dismorphiinae, Pierinae, and Coliadinae at least), Nymphalidae (Danainae, Morphinae including *Caligo*, Nymphalinae at least), and Libytheidae, and eggs were upright, both traits as in Noctuoidea.

Family Branching Sequence

Before proceeding to the butterfly phylogenetic tree and detailed enumeration of associated character changes, justification for the sequences of branches must be given. For this analysis, we can start with a partial tree, with Hesperidae branching from the base, and the tree then forking into Papilionidae and Nymphalidae-Libytheidae. Virtually everyone who has ever written on butterfly phylogeny has accepted this partial tree. The points of origin of Pieridae and of Lycaenidae must now be ascertained on this partial tree.

Origin of Pieridae

Ehrlich (1958b) found that Pieridae are most similar to Papilionidae morphologically. But Kristensen's (1976) cladistic analysis placed the origin of Pieridae from the stem of Nymphalidae-Lycaenidae rather than the stem of Papilionidae. The following characters (denoted by small letters) support the origin of Pieridae from the Papilionid line: the secondary sternopleural sulcus (sss) (of Brock, 1971; = precoxal suture of Ehrlich, 1958b) (Fig. 1) is weakly developed in skippers (Kristensen, 1976 discards this character because he and Brock did not realize that it is present in skippers; my dissections show it in *Erynnis*, *Epargyreus*, etc.). Brock illustrates it in skippers and labels it the "upper sector of the precoxal suture", which is a misinterpretation, as this sulcus ("suture") arises from the rear of the anapleural cleft in all moths. Phylogenetically, the upper sector of the paracoxal ("precoxal") sulcus very doubtfully crept down the pleural sulcus to form the sss, because the pleural sulcus is an internal strengthening ridge and does not need the assistance of such a creeping rudiment. In skippers the sss strengthens the ventral

edge of a slight dome in the episternum. The sss seems homologous in Hesp.-Nym.-Lyc. (Hesperiidae-Nymphalidae-Lycaenidae). The secondary sss has (a) become lost in Pier.-Pap. (Pieridae-Papilionidae), but (b) in Nym.-Lib. (Libytheidae)-Lyc. it is strongly developed and usually also runs behind the pleural sulcus, (c) forming an area called the preepimeron (present in Nymphalidae and Lycaenidae).

In skippers, scutum 3 is somewhat visible from the rear, but (d) in Pap.-Pier. (Papilionidae-Pieridae) scutum 3 is scarcely visible from the rear, and (e) in Nym.-Lib.-Lyc. scutum 3 is very visible from the rear. These shape differences may have affected (or resulted from) flight behavior: most of the Pap.-Pier. patrol to locate mates, whereas many of the Nym.-Lib.-Lyc. perch (Scott, 1975). (f) The prothorax presternum is absent in Pap.-Pier. but present in Nym.-Lib.-Lyc. (and seems to occur in Hesperiidae). Several weak characters, internal prothorax structures, are similar in most Pap.-Pier.: (g) the furcal arms have a secondary anterior lamella or prong (absent in *Baronia*), (h) the intercoxal lamella has migrated back to the furca (see Ehrlich, 1958b, Figs. 29, 30) except in *Baronia*, and (i) the discrimen generally (but not in Baroniinae or Parnassiinae) has an anterior spine or lamella. (j) The retina cells are cross-shaped in cross-section in Pap.-Pier., but rosette-shaped in other butterflies (Yagi and Koyama, 1963). (k) The radial plate on the forewing base seems to be hardened posteriorly in the same manner in Pap.-Pier. (1) The spinasternum is expanded laterally in front of the spina in Pieridae and most Papilionidae (but this is a weak character, as *Baronia* (Pap.) lacks the expansion, and in Pieridae the expansion is much less, see Ehrlich, 1958b). (m) The labial sclerite is often membranous in Pap.-Pier., sclerotized in Nym.-Lib.-Lyc. (however it is membranous in front of the palpal sockets in Pap., behind them in Pier. The primitive state may be membranous as in most *Hesperiidae* (Miller, 1971), in which case the membranous labial sclerite of Pap.-Pier. and Styginae may be primitive as well). (n) The female has a cover-flap over the mating tube in Pap.-Pier., which I have not seen in other families (however this is another weak trait, as the flap is now limited to Papilioninae, Pierinae, and Coliadinae). (o) A frontoclypeus-proboscis muscle is present in some skippers and in Pap.-Pier., but is absent in Nym.-Lib.-Lyc. (character 3 of Ehrlich and Ehrlich, 1962). (p) The male forelegs are normal size and fully functional in Pap.-Pier., smaller in Nym.-Lib.-Lyc. Antennal cleaning is done by the middle legs of both sexes of Nymphalidae and Lycaenidae, but by the forelegs of Pap.-Pier.-Hesp. (Hesperiidae) (Jander, 1966). (The epiphysis of Pap.-Hesp. is an antenna-cleaning device. Another such device developed by Lycaenidae is a scale tuft on the mesothorax femur and an opposable grooved scale brush on the tibia, which remove debris as the antenna is passed through the flexed leg; Libytheidae have a strong femur tuft but it is small in Nymphalidae, and both families plus some Riodininae have a weak or absent tibial brush.) Jander found that even the Lycaenidae with large forelegs use the middle leg for cleaning, which proves that the ancestor of Lyc.-Lib.-Nym. had a small foreleg and thus developed middle-leg cleaning. Detection of sugar for feeding is by the forelegs of Pieridae (and undoubtedly Papilionidae), but by the middle legs of Nymphalidae (and presumably Lib. and Lyc.) (Frings & Frings, 1956). (q) The tiny spines all along the top of the tarsi are present in Pap.-Pier., but absent in Castniidae, Hesperiidae and Nymphalidae (except for *Dioriste*, Satyrinae, an unusual convergence, and the fine dorsal spines of Ithomiinae, Forbes, 1939)—Lib.-Lyc. (except for *Iraota* and *Amblypodia*,

Lycaeninae, also convergence). Kristensen (1976) cites this as a derived trait of Nym.-Lyc., but actually it is a derived trait of Pap.-Pier., and spines are absent in moths and skippers. (r) The eyes are hairy in many Nymphalidae and Lycaenidae, bald in Pap.(except *Bhutanitis mansfieldi*)-Pier., a weak character. (s) The papillae on the tip of the proboscis (taste organs) tend to be larger in Nym.-Lib.-Lyc. than in Pap.-Pier. (Ehrlich, 1958b), but this seems to be a weak character owing to variation among genera. (t) Forewing vein M_2 is close to M_3 (a "quadrifid cubitus") in Papilionidae and some Pieridae (Dismorphiinae), and Klots (1931) suggested that this venation is primitive in Pieridae. This seems to be a weak trait, as the other Pierid subfamilies differ, and have a more Nymphalid-like venation. (u) The spinasternum is much more heavily sclerotized between its two main points of attachment to the mesothorax in Pap.-Pier. than in other families. Pupae of Papilioninae and Pierinae commonly have both green and brown forms, but this may be convergence (*Nymphalis urticae*, Nymphalidae, also has these forms).

The following characters support the origin of Pieridae from the Nymphalid-Libytheid line: (v) A prothorax muscle from the spinasternum to the coxa (character 11 of Ehrlich & Ehrlich, 1963) is present in Hesp.-Pap., but lost in the others. (w) The epinasternum is present in Hesp.-Pap., but lost in the others. (x) The antenna club is pendulum-shaped in many Pier.-Nym.-Lib. (a very weak character that undoubtedly arose independently, as many other genera of Pier.-Nym. have rodlike clubs). (y) The maxillary palp is one-segmented or absent in Hesp.-most Pap.-Pier.-Nym.-Lyc., and two-segmented in one Papilionid genus (*Baronia*). Kristensen placed this character here, but it seems very weak, because it is one-segmented in Hesperidae. *Baronia* probably reacquired a two-segmented rudiment. (z) In Noctuidae, Hesperidae, and Papilionidae the papilla analis apophysis retractor is attached to segment 7, but in Pier.-Nym.-Lyc. it has shifted to segment 8 (Stekol'nikov, 1967; though the tree adopted by Stekol'nikov is identical to that of Fig. 3). Brock (1971) stated that Pier.-Nym.-Lyc. have a wide secondary sclerite on the metathorax scutellum, and Kristensen cited the character here. However, I dissected examples of every family and could not find this structure, nor did Ehrlich find it; it is not defined by either membranous boundaries or by internal ridges (sulci). Chapman (1895) stated that the pupal abdomen of Pier.-Nym. moves only laterally, whereas the abdomen of Hesp.-Pap. can move in all directions; this seems a very weak character, as the *Papilio* abdomen seems rather rigid, moving only at joint 4-5 (weakly at 5-6), and the *Papilio (brevicauda)* pupae I disturbed wiggled the abdomen only laterally.

If the weak characters are given half a point and others one point (although character p may represent three characters), then $17\frac{1}{2}$ characters support the origin of Pieridae from the Papilionid line and only three support its origin from the Nymphalid-Libytheid line. Some of these characters represent loss of a trait rather than a new development, and it is generally much easier to lose a trait than to originate it. A taxon is probably monophyletic if it has some unusual derived traits. Pap.-Pier. has many traits that may qualify (g, h, i, j, k, l, n, q, t and u—some of these are weak characters), and Nym.-Lib.-Lyc. has some strong characters (b, p, r, s), whereas the Pier.-Nym.-Lib.-Lyc. has no strong characters. The few characters supporting the latter grouping represent losses of structures, or are weak.

Origin of Lycaenidae

Lycaenidae undoubtedly arose from the Nym.-Lib. ancestral line. Eight charac-

ters support this origin of Lycaenidae (b, c, e, f, o, p, q, r, s—the last two are weak traits each counted $\frac{1}{2}$). Four traits support the origin of Lycaenidae from the stem of Papilionoidea before the Papilionidae and Nymphalidae ancestors diverged: (A) A metathorax muscle is fan-shaped in skippers and Lycaenidae, but more parallel-sided in all other families (pterothorax character #13 of Ehrlich & Ehrlich, 1963). Evidently the Pap.-Pier. and Nym.-Lib. ancestors independently developed a parallel-sided muscle. (B) First-stage larvae of skippers and Lycaenidae have annuli (chitin rings), which other families lack. These annuli may be glands in Lycaenidae (Wright, 1983 notes perforations in the dome-shaped top of the cone-shaped ring of the annulus "lenticle" of *Lycaena* third and fourth instars—are annuli related to the "perforated cupolas" of Malicky, 1970?), are doubtfully vestiges of lost setae, and apparently evolved independently. (C) The mesothorax discrimen dips down to the base of the furca in skippers and Lycaenids, but extends straight back to the furca in all other butterflies (except it curves slightly down in *Baronia*). The metathorax discrimen dips to the furca base in all skippers and nearly all butterflies (except *Pseudopontia*), so the Lycaenids may have regained the ancestral form by using metathorax genes. (D) Chapman (1895) notes that pupal setae are prominent on Hesp.-Lyc., absent or small on Pap.-Pier.-Nym. (though minute in some such as *Limenitis*); no doubt the setae were generally lost in the latter groups, which are more exposed and colorful (Nymphalinae and Acraeinae pupae have various cones or scoli, of course). Only one trait supports the origin of Lycaenidae from the Pap.-Pier. ancestral line: (E) pulvilli are single in Lyc.-Pier. (absent in Papilionidae), but forked in all other families, which undoubtedly represents independently derived states of fusion of the forks.

Evolution of Skippers (Hesperioidae)

Skippers were the first group to split off of the butterfly line (Fig. 3), probably in the Cretaceous period. Skippers kept most of the traits of the butterfly-skipper ancestor (but at least some other butterflies lost some of them). After skippers branched from the line leading to Papilionoidea, they evolved some new traits. The hindwing discocellular veins were largely lost in skippers, and vein M_2 became weak or absent. The humeral vein became pointed toward the wing base, and the wing edge (costa) thickened at the base. A stigma may have occurred on the male forewing, as a discal stigma is present in Coeliadinae, Hesperinae, and "Trapezitinae." The antenna club of skippers is perhaps a modification of the enlarged and hooked antenna found in most Sphingidae; if not, the ancestral skipper must have developed a bent club as in Pyrginae, and the Hesperinae and other clubs are modifications. An "eyelash" of scales on the base of the antenna developed in at least some skippers. The orbit of the eye became wider, and developed (functional?) tiny ommatidia (Ehrlich, 1960), perhaps a unique trait in Lepidoptera. The skipper head became very wide. One could hypothesize that the wide head and the rudimentary ommatidia in the orbit are due to a nocturnal butterfly ancestor becoming diurnal. In moths, newly arisen diurnal species evolved a smaller eye (rudimentary ommatidia being a transition stage?) and a wider face (Ferguson, 1971 p. 9-10); however, Ferguson notes that this apparently happens quickly, even between closely related species, whereas skippers have had much more than 50 million years to improve their eye. Horridge (1975) found that the skipper eye has a clear zone between the lens system and retina and truly focuses

light, as in many nocturnal moths, and skippers share with Bombycoidea retinula cell extensions to the lens system, and skippers share with Agaristinae (Noctuidae) an absence of pigment in the clear zone in the daytime. Because Agaristinae and some Bombycoidea are diurnal, a nocturnal butterfly ancestor is not required, and, based on Horridge, the rudimentary lenses in the skipper orbit would help focus the eye at its periphery (Papilionoidea lack a clear zone and do not have focused eyes).

Patches of sense-hairs (chaetosema) often developed on front as well as the rear of the head (Jordan, 1923; only the rear patches are in other butterflies, except *Phoebis*). The spurs on the middle leg tibia were lost (and the upper spurs on the hind leg tibia were later lost in some skippers). The tergal bar connecting the abdomen to the thorax is derived from tergum 1, but it became fused to tergum 2 (with no gap or sulcus at the point of fusion, a trait unique or nearly so). The adult peritrophic membrane delaminated from the midgut epithelium instead of the front of the midgut (Waterhouse, 1953). The larvae developed the habit of living in a leaf rolled and silked into a tube, which provided the selective basis for developing (or perhaps retaining) crochets in a complete circle in mature larvae (because the outer crochets can grip the nest). The larval neck became narrow (except in Giant Skippers), to allow the head to swing about inside the leaf nest to silk it into a tube. Some pupae are suspended inside the larval leaf nest by a Y-shaped silk girdle (the cremaster is not attached strongly). As other adaptations to this habit, the larvae seldom wander like other butterflies before pupation, and the mature larvae developed powder glands beneath abdomen segments 7 and 8 to provide water repellent powder for the pupa in the nest. First-stage larvae developed hardened rings (annuli) on the body, which may be glands; they have only primary setae, which are usually enlarged or forked at the tip. Older larvae have only short setae, and have no spines or antlers, although some Hesperinae have conelike horns and two fleshy tails.

Early in their evolution, skippers split into two groups. This basic division is obvious, but the remaining evolution of skippers is rather obscure (see Miller, 1971). The first group switched to monocotyledons (grasses, etc.) for food, the antenna club stayed oval with a small pointed tip, a peculiar unique basking posture evolved (the hindwings are spread much more than the forewings), the base of forewing veing M_2 moved closer to vein M_3 than to M_1 (it varies in "Trapezitinae"), and first stage larvae lost the second SD seta on thorax segments 2-3. This ancestor produced the Megathyminae, which are borers in Agavaceae, and the Hesperinae. The Megathyminae adult head became smaller, the larval prothorax became wider, the first stage larval hairs grew longer, and the plateau behind the thorax spiracle on the pupa disappeared. I include the Trapezitinae in the Hesperinae because, based on Evans' (1949) findings, it seems unlikely that Hesperinae is a monophyletic group if Trapezitinae is excluded from it. Trapezitinae are weakly characterized by having the end of the hindwing discal cell sloping toward the body. Megathyminae have often been treated as a distinct family, but there is no doubt that they evolved from this monocotyledon branch of skippers. Furthermore, it is possible that they too are merely an unusual offshoot of Hesperinae, cladistically. Within Hesperinae, the *Carterocephalus* (America-Eurasia)-*Heteropterus* (Eurasia)-*Astictopterus* (Africa) group of Evans (1937-1955) may be the most distinct group.

The second group of skippers ate dicotyledons (some *Urbanus* later switched to monocotyledons), the antenna club became mostly boomerang-shaped, and the base of forewing vein M_2 was the same distance to vein M_3 as to M_1 . The male hind-leg tibia developed a hair pencil that fits between the abdomen and a posterior extension of the metepimeron (this extension a mere long scale tuft in *Celaenorrhinus*), traits now present in Pyrginae and Coeliadinae. Pyrginae often have characteristic sex glands (a male costal fold, female glands on top of abdomen segment 7, and female abdominal hair pencils). Coeliadinae have the second palp segment stout and erect, the third segment long and projecting forward; the antenna is Pyrginae-like. Pyrrhopyginae developed a shortened abdomen, a more triangular hindwing, an antenna having most of the club beyond the elbow, a very long forewing discal cell, and apparently lost the hind leg hair pencil (or never had it). Whether these three subfamilies are really monophyletic entities remains to be seen. Pyrrhopyginae is probably monophyletic, but it and Coeliadinae are probably just two of the many branches of Pyrginae if principle #2 above is applied. W. Evans (1951-1955) suggests that the ancestor of Pyrrhopyginae and Coeliadinae occurred throughout the tropics when Africa and South America still touched, but when they split the American population became Pyrrhopyginae and the Old World population became Coeliadinae. However, de Jong (1983) states that Coeliadinae and Pyrrhopyginae are not phylogenetically related. de Jong (1975) also shows that the *Telemiades* and *Erynnis* Pyrgine groups of Evans are really just one group.

Unfortunately there is no adequate tribal classification of skippers, and new characters are needed, as the current classification relies too heavily on antennae and palpi.

Evolution of the Ancestor of Papilionoidea

The branch producing the Papilionoidea after the Hesperidae branched off (Fig. 3) lacked the specialized traits of skippers such as larval powder glands and leaf nest building, and the mature larva wandered before pupating. This branch changed to some extent before splitting. The forewing R veins began to join with each other. (The frenulum and retinaculum were apparently lost earlier, by the ancestor of skippers and Papilionoidea.) The antenna club remained straight, but any angled tip present on the Papilionoidea-Hesperioidea progenitor was lost. The internal structure of the compound eye changed slightly (Yagi, 1953). The orbit of the eye shrank to (or had) a narrow rim lacking ommatidia, extensions of the rhabdoms and pigment ran through the clear zone of the focused skipper eye, the eye shrank on the back of the head, and the transoccipital band seems to have moved more mesally. The temporal sulcus on the head (apparently homologous to the temporal ["epicranial"] cleavage line of Hesperidae pupae and the temporal sulcus, or "transverse suture" of Miller, 1971, in the Hesperiid adult) changed course (often parallel to the paratemporal sulcus, but perhaps the position in *Lycaena* is primitive). A "laterofacial sulcus" no longer ran ventrally from the frontogenal sulcus as it does in Hesperidae and various moths including Castniidae. The front rim of the first adult thorax spiracle became mostly desclerotized. The upper pair of spurs of the hindleg tibia was lost, leaving the lower pair on the hindleg and middle leg. On the prothorax the parapatagia became membranous, and the lateral plates of the pronotum developed a Y-shaped structure where they join dorsally.

On the mesothorax the paracoxal sulcus joined the marginopleural sulcus (Fig. 1) (in Hesperidae they rarely touch in some genera such as *Capila* but are not fused into one sulcus) (in Curetinae, Lycaenidae, a sulcus extending dorsally from the marginopleural resembles the paracoxal sulcus of skippers but is undoubtedly independently derived). The mesothorax anepisternum became small and the hypopteron extended upward farther, and the postcoxal sclerite on the meron moved to the rear. In the mesothorax the discrimen grew straight back to the furca. The metathorax phragma grew larger (later developing stalks or lobes), and the transphragma lost the two laminae of Castniidae and skippers. The posterior ventral lamina (of Brock, 1971) on the metathorax furca disappeared (among Hesperidae it is small in *Agathymus* and large in *Epargyreus*, extending to the foot, but is not discernible in Papilionoidea). On the front of the midgut the cardia became obvious externally (Homma, 1954). On older larvae the crochets were lost (or, probably, were never present) on the outside of the prolegs (the few outer crochets in Riodininae and Libytheidae and the *Papilio troilus* group at first seem to be rudiments of the ancestral circle, but may be new developments, as young larvae have them, and the Macrolepidopteran butterfly ancestor may have lacked them in older larvae). Mosher (1916) suggested that Hesperioidea pupae might have dorsal movement between abdomen segments 3-4 unlike Papilionoidea, but this is doubtful (not true in pupae I have examined), and the wingtips cover segment 4 ventrally in both groups so any movement of segment 4 is doubtful. The pupa lost the temporal cleavage line between the antenna bases ("epicranial suture" of Mosher, 1916; she listed it in Lycaenidae where it is actually absent, as I cannot detect it). (In skip per the temporal cleavage line is obvious, and each vertex half (on the head) behind the cleavage line remains attached to its thorax pronotum half after adult emergence. Furthermore, the skipper eye-pieces remain attached to the gena of the head, which in turn remains loosely attached to the base of the proboscis (galeae), contrary to Brock, 1971, p. 93.)

The Evolutionary Origin of the Five Families of Papilionoidea

At this point, the Papilionoidea line split in two (Fig. 3). The line leading to Papilionidae and Pieridae developed large wings compared to the body (perhaps contributing to the trend that males of most species of these families patrol to find females, Scott, 1975). The metathorax changed in shape so that the scutum is only slightly visible from the rear (which perhaps altered their flight, also favoring their patrolling behavior). The forewing vein M_2 was apparently close to vein M_3 (a "quadrifid cubitus", primitive in Pieridae according to Klots, 1931, although most subfamilies lack this trait). The radial plate on the forewing base (Fig. 2) became hardened on the rear in the same way. The retina cells of the compound eye became cross-shaped at each level (Yagi and Koyama, 1963). The tarsi developed several rows of dorsal spines (all butterflies have ventral spines). On the prothorax the presternum was lost, the internal keel (discrimen) developed an anterior spine or ridge, the keel migrated back to the furca, and the arms of the furca also developed an anterior ridge or prong. The spinasternum became much more heavily sclerotized between its two main points of attachment to the mesothorax than in any other family. On the mesothorax the secondary sternopleural sulcus disappeared. The internal muscle connecting the metathorax scutum to the phragma in front of the abdomen became more rodlike (pterothorax character #13 of Ehrlich and Ehrlich, 1963). Abdomen tergites 2-3 possibly lost some movement between

them (tergites 1-2 are always fused in Hesperioidea and Papilionoidea) though this trait is doubtful because *Parnassius* has complete movement. A cover flap apparently developed above the female's mating tube or developed later (it is present in Papilioninae, Pierinae, and Coliadinae). Larvae probably ate Leguminosae.

This phyletic line then split into the Papilionidae and Pieridae ancestors (see below).

The ancestral line leading to Nymphalidae, Libytheidae, and Lycaenidae (Fig. 3) kept smaller wings in relation to the body for more maneuverability, so, as in skippers, males of many species perch to find females (Scott, 1975). The metathorax changed in shape so the scutum became very visible from the rear, which may have contributed to their perching behavior. The eyes probably became hairy, as many Nymphalidae and Lycaenidae have hairy eyes. A muscle from the proboscis to the frontoclypeus was lost (character 3 of Ehrlich and Ehrlich, 1962). The male forelegs became small and nearly useless (some Lycaenidae later reacquired larger segmented and clawed male forelegs perhaps by using female or mesothorax genes, see Lycaenidae); Jander (1966) found that the middle legs clean the antennae in both sexes of Nymphalidae and Lycaenidae, and Frings and Frings (1956) found that the middle and hind legs detect sugar in Nymphalidae (the front and middle legs detect it in Pieridae). The middle leg apparently developed an opposable femur tuft and weak tibial brush for antenna cleaning (both structures were later lost in some Riodininae and a few Lycaeninae, and in Nymphalidae the femur tuft is weak and the tibial brush absent or very weak). The epiphysis on the foreleg was lost. On the prothorax, a muscle from the spinasternum to the leg coxa was lost (prothorax character #11 of Ehrlich and Ehrlich, 1963). On the mesothorax the secondary sternopleural sulcus (Fig. 1) became well developed, and part of this sulcus developed behind the pleural sulcus, forming a space called the preepimeron. The papilla analis apophysis retractor shifted from segment 7 to 8 (Stekol'nikov, 1967).

At this point in evolution, the Lycaenidae probably branched off (Fig. 3, see Lycaenidae below).

The line leading to Nymphalidae and Libytheidae (Fig. 3) underwent further changes. The antennae developed three ventral ridges (these and other butterflies have antennal grooves, but other families lack the ridges), and the antenna often became pendulum-shaped. Inside the head a third muscle developed from the sucking pump to the antenna ridge (character #12 of Ehrlich and Ehrlich, 1962; these muscles vary and some Nymphalidae have lost one or two of the three). The male forelegs became very small. Two muscles from the head tentorium to the cervical sclerite became distinctly separated (prothorax character #2 of Ehrlich and Ehrlich, 1963). A muscle from the metathorax scutum to the phragma in front of the abdomen became more rodlike (pterothorax character #13 of Ehrlich and Ehrlich, 1963). The silk girdle around the pupa was lost, and the pupa now hung only from the cremaster. The visible legs on the pupa all touched the eye. The pupal thorax spiracle changed into a slit.

Now the Libytheidae split off into a separate line, and the Nymphalidae evolved further (Fig. 3; see those families below). Kristensen (1976) suggests, without evidence, that Libytheidae evolved from one of the subfamilies of Nymphalidae, and so should be included in Nymphalidae. However, larval traits suggest that Libytheidae evolved first, and kept an ancestral type of larva, while the

Nymphalidae then evolved small adult female forelegs, and evolved numerous larval spines, antlers, filaments, and tails. The trend in Nymphalidae larvae is toward the development of extra setae and structures, whereas Libytheidae has lost several primary setae that were present in the Papilionioidea ancestor. The larvae of Nymphalinae have an enormous set of spines and antlers, and it seems impossible to derive Libytheidae larvae from them. Some first stage Satyrinae larvae (*Cercyonis*) have only one SD seta on thorax segments 2-3 as in Libytheidae, but these setae are vastly different in shape, and the older larvae and adults are much different. Deriving the Libytheidae from Danainae or other Nymphalidae seems equally difficult. Danainae lack horns and spines on larvae, but they have extra setae in the first stage larvae, and have fleshy filaments, plus specialized adult mating behavior, that make it extremely doubtful that the other Nymphalidae or Libytheidae were derived from them. Libytheidae have small patagia, whereas they are large in all Nymphalidae, membranous in Lycaenidae. The venation of Libytheidae is similar to that of Nymphalinae (Nymphalidae) and Styginae (Lycaenidae) so are of no help.

Evolution of Papilionidae

Papilionidae evolved from a common ancestor with the Pieridae (Fig. 3). After they split off of the Pierid line, the fw vein 2A ran to the hind margin instead of joining 1A. The second median plate (Fig. 2) was lost on the forewing base. On the head the labial sclerite usually became membranous in front of the palpi. The two cervical sclerites became joined beneath the neck. The spurs were lost on the tibia of the middle legs, and the pulvilli and arolium were lost on the legtips. The horizontal chamber of the adult aorta lost its enlargement and its two ostia (Hessel, 1969). The anepisternum was later often lost by various genera. On the metathorax the meral sulcus developed. Inside the thorax the topmost front-to-back wing muscle became larger than the others (pterothorax character #4 of Ehrlich and Ehrlich, 1963), and a muscle from the phragma of postnotum 2 to the abdomen base became tapered as it extends downward to the abdomen (pterothorax character #5 of Ehrlich and Ehrlich, 1963). The apophysis on abdomen segment 8 is not known in female Papilionidae (though its occurrence is spotty within other families). The larva developed the osmeterium to repel ants and other predators with the chemicals isobutyric acid and 2-methyl butyric acid (these chemicals present in *Baronia*, *Papilio*, *Eurytides*, Eisner et al., 1970; other chemicals are present also, Honda, 1983), and lost the ventral neck gland. The first-stage larva developed many extra setae on the side and above the prolegs, a trend that continued later and extended onto the head in some groups.

The Baroniinae (one Mexican species *Baronia brevicornis*) split off at this point, and developed some peculiarities, including many secondary body setae and many forked setae on the bumpy first-stage larval head (Ruiz, 1969; Vasquez and Perez, 1961), the antenna lost its scales, veins Sc and R₁ joined together on the forewing, one R vein disappeared, the tegumen and uncus became fused, the mesothoracic discrimen curved down in front of the furca slightly, and the prothorax furca arms lost the secondary anterior prong or lamella. *Baronia* retains a Pierid-shaped larva, a Parnassiinae-shaped pupa in an earthen cell, and feeds on the legume, *Acacia*. The Eocene fossils of *Praepapilio* were placed in a new subfamily by Durden and Rose (1978), but their poor state of preservation makes this doubtful (the

presence of CuP is especially dubious and the fore- and hindwings overlap confusingly in the fossils; they are best placed in Baroniinae, or perhaps in some other butterfly or Macrolepidoptera family.

In the remaining Papilionid line, vein 3A was lost on the hindwing (probably because of a scent fold which developed in that position, possessed now by *Eurytides* and *Parides* etc., which was later lost in Parnassiinae and scattered Papilioninae). In the prothorax, the spinasternum widened at the spina, the furcal arms developed a secondary anterior lamella or prong, and the intercoxal lamella migrated back to the furca, if the Papilionid ancestor lacked these three traits. Older larvae had red spots, tubercles, and ate *Aristolochia* (modern groups with tubercles and usually red spots are Parnassiinae: all Zerynthiini, and *Archon* in Parnassiini; Papilioninae: all Troidini, and in Leptocircini the *Protesilaus lysithous* group, perhaps *Graphium* which have spines on the thorax and rear, and some Papilionini which have small tubercles). Adults probably had a tail on vein M_3 and a female sphragis.

The Parnassiinae branched off here, and developed some unusual traits: mature larvae developed a carpet of setae and their osmeteria became non-functional (at least in *Parnassius*), the tarsal claws became asymmetrical, and females possessed a sphragis (five of eight genera now have it, as do some Papilioninae tribe Troidini). In at least *Parnassius*, two hooks developed on the forewing base (on the base of R and on the radial plate) to aid emergence of the adult from the silked or underground pupation site (the other genera should be examined for this trait). Two tribes, Zerynthiini and Parnassiini, are well founded (Ehrlich, 1958b; Hancock, 1983), though some traits Hancock cites are weak or have exceptions (patagia). Zerynthiini lost the scales on their antennae and legs; Parnassiini lost the tails, the larva pupates in debris or soil with a weak "cocoon", and the humeral vein became simple, the palpi a bit shorter.

The remaining line (Fig. 3), which became the Papilioninae, grew very large in size, adults continue to flutter while feeding at flowers (apparently an adaptation to their weight), the CuP vein ("cross-vein" or "basal spur") developed on the forewing base, probably to strengthen the larger wing (it is present in all butterfly pupae (Zeuner, 1943) but is rare in adults; in other butterflies a trace is present in Zerynthiini (Hancock, 1983), *Heliconius* (Emsley, 1963), etc.), and vein M_2 moved closer to M_3 than it was (M_2 was fairly close to M_3 in the Pap.-Pier. ancestor). The prothorax discrimen developed an anterior spine (if it was absent in the Papilionid ancestor). The pupa developed two blunt bumps on the head, and a dorsal thorax protuberance. Larvae retained fleshy filaments from the Parnassiinae ancestor. During the evolution of the Papilioninae, the first stage larvae acquired more and more extra setae, some of them on fleshy bumps (scoli).

The tribes within Papilioninae are still not very well founded despite the work of Ehrlich (1958b), Munroe (1961), and Hancock (1983). The controversy involves where Papilionini (P) arose, from the Leptocircini (L; = "Graphiini") stem or the Troidini (T) stem. The following traits support the origin of Papilionini from the Troidini stem, where Hancock places it: antenna unscaled in P and T, scaled in L; legs unscaled PT, scaled L; superuncus ("pseudouncus") always replacing uncus PT, seldom replacing L; patagia membranous or nearly so PT, largely sclerotized in most genera of L. The following traits support the origin of Papilionini from the Leptocircini stem: many secondary setae on first instar larvae (especially on the

head of *Papilio*; *Eurytides* and *Battus* have few secondary setae on the head; Troidini has fewer on the body than the others) in LP, fewer in T, perhaps a weak trait; mature larvae have red spots and tubercles in T, often lack them in LP, a weak trait; hostplants usually Aristolochiaceae in T, never Aristolochiaceae in LP, a weak trait. The tentorial crests are progressively higher in P, T, and L, the only trait favoring the split of Papilionini before Leptocircini and Troidini split. Thus Hancock's scheme has the most support, and another trait, the spine on the prodiscimen present in Papilionini and Troidini (except *Battus*) fits this scheme imperfectly. However, most traits supporting the scheme represent losses of structures, so doubt remains. Other traits, including pigments, pupal shape, discocellular vein position, humeral vein, precostal cell, metathoracic discimen, signum, anal fold scent glands, and tibia-tarsi spining, are too variable or the differences too weak for them to be useful in tribal classification. (The character used to separate Papilionini and Troidini in most keys, tibial and tarsal spining, seems useless, because different legs, or inner and outer faces of the same leg, have as much variation in spining as the variation between tribes, and some *Battus philenor* legs I examined have a spineless impressed lateral space, contrary to Munroe's and Hancock's keys.) Setal patterns on first-stage larvae should be studied much more. The Troidini (*Battus* at least) switched osmeteria chemicals (they have beta-selinene and selin-11-en-4 α -ol, instead of isobutyric acid and 2-methyl butyric acid possessed by Baroniinae and Papilionini, Eisner et al., 1970; Burger et al., 1978).

Hancock's paper (1983) is a worthwhile contribution on Papilionidae, following cladistic principles based on largely the same characters used by Ehrlich and Munroe. However, Hancock's invocation of a special set of weak characters to create six genera out of the single genus *Papilio*, characters different from those used to distinguish other genera of Papilioninae, surely is an act of "special creation". In order to make the genera of Papilionini comparable to those of other tribes these six genera should be returned to subgenera of *Papilio*. Minor points concerning Hancock (1983) are these: *Præpapilio* is from the Green River Shale, not from Florissant, the meral sulcus is characteristic of all Papilionidae, and Parnassiinae lack a prodiscimen spine. The antenna of Parnassiinae is 11.5 mm or shorter, the antenna of Papilioninae is 11.0 mm or longer. Some of Hancock's "derived" traits may well be primitive (the red-tuberculate larva, long palpi). Hancock states that the "precoxal suture" (my secondary sternopleural sulcus) was present in the Papilionid prototype, based on Ehrlich's (1958b) mention of it in Parnassiinae; but it is not on the Parnassiinae I have examined and doubtfully occurs in any Papilionid.

Evolution of Pieridae

Pieridae evolved from the line that also produced Papilionidae (Fig. 3). After the Papilionidae branched off, the wings of the Pieridae ancestor probably were colored with pterin pigments (the whitish, yellowish, and orange pigments present in most species, and in other butterflies as well). The antenna muscles developed a forward slant (character #10 of Ehrlich and Ehrlich, 1962). The antenna later became pendulum-shaped in some groups. On the head the labial sclerite often became membranous behind the palpi. Several R veins on the forewing branched from each other. The claws on the leg tips forked in two (which happened in some

other families also, namely *Lamproptera curius* and *Meandrusa* in the Papilioninae, Acraeinae, and Aphnaeini in the Lycaeninae). The pulvilli (that were forked) joined into one wide pulvillus. The epiphysis on the foreleg was lost. On the prothorax, the two lateral plates of the pronotum became fused together only at the top (Ehrlich, 1958b), a muscle from the furca to the cervical sclerites was lost (prothorax character #1 of Ehrlich and Ehrlich, 1963), a muscle from the spinasternum to the coxa was lost (prothorax character #11 of Ehrlich and Ehrlich, 1963), and the spinasternum became widened into an oval in front of the spina. In the mesothorax the anepisternum was lost and a muscle to the postcoxal sclerite became attached to the scutum farther back (pterothorax character #6 of Ehrlich and Ehrlich, 1963). On the abdomen the prespiracular bar was lost, and sternum 2 moved forward more than in other families (though almost as far forward in Hesperidae). The papilla analis apophysis retractor muscle shifted from segment 7 to 8 (Stekol'nikov, 1967). The pupa developed a single cone on the head, and the pupal wings probably expanded somewhat (see Aiello, 1980 for Dismorphiinae). The first-stage larva lost the second SD seta on the metathorax. Setae D1 and D2 of young larvae are forked and dispense honeydew (Forbes, 1916) to bribe ants (in Dismorphiinae, Coliadinae, and Pierinae at least, Ford, 1945).

The ancestor of Dismorphiinae and Pseudopontiinae branched off the Pieridae line at this point (Fig. 3). The patagia on the prothorax became membranous, and the peculiar male mating structures unique to both groups developed (tegumen short, uncus in two lobes, valvae fused ventrally). This ancestor was probably in both Africa and South America when they were joined; then, after the continents split apart, the African population ancestral to Pseudopontiinae developed rounded wings and a peculiar pattern of fusion of some wing veins (and lost two R veins), developed a linear (unclubbed) antenna, and the metathorax discrimen grew straight back to the furca (as in the mesothorax), while the American population ancestral to Dismorphiinae (of which one genus probably later spread to Eurasia across the Bering Strait) kept all five forewing R veins, but they joined up to one stalk (Dismorphiinae have other peculiarities also, including a very wide juxta, and only one SD seta on both mesothorax and metathorax, the major setae T-shaped). Dismorphiinae retained the forewing vein M_2 closer to M_3 of the Papilionid-Pierid ancestor (see Klots, 1931), while in the other Pierid subfamilies M_2 moved toward M_1 . Pseudopontiinae contains just one species, *Pseudopontia paradoxa*, a rounded-wing white West African forest species.

After those subfamilies branched, the ancestor of Pierinae and Coliadinae developed a tiny bump on the forewing base (which Sharplin, 1963a calls a remnant of the M vein) that separates the base of the Cu vein from the radial plate, a trait unique to Pierinae and Coliadinae among the butterflies and skippers (Sharplin, 1964 claimed that all Papilionoidea have it, but she examined only *Pieris*; I examined the other subfamilies and families for this trait). First-stage larvae lost the second prothorax L seta. Females developed unique lobelike scent glands on the female abdomen tip to repel males (females spread the wings and raise the abdomen to waft the scent). This line then split into Pierinae and Coliadinae. The Pierinae developed a more clubbed antenna (usually) and a longer tegumen, the patagia became membranous, and the uncus hinges on the tegumen, flexing down and forward (in *Pieris* and *Anthocharis*, Stekol'nikov, 1967; *Neophasia*, this paper). The Coliadinae nearly lost the humeral vein, the last palp segment shrank, a "raised line" developed (Klots, 1931), and the juxta expanded at the tip.

Anthocharis and *Euchloe* have sometimes been placed in a different tribe ("Euchloini", Klots, 1931) or even subfamily, but their similarity in morphology (Ehrlich, 1958b), appearance, habits, and Cruciferae hostplants to *Pieris* places them in the Pierinae. Geiger (1981) studied 20 different body enzymes of 23 species of Pierinae, Coliadinae, and Dismorphiinae, and found that the differences between *Anthocharis* and other Pierinae are equivalent to the differences between other genera of Pierinae. Stekol'nikov (1967) thought that the similarity of "Euchloini" and Pierini in genital musculature indicated very close relationship.

Evolution of Nymphalidae

Nymphalidae evolved from the ancestral line that produced Lycaenidae and then Libytheidae (Fig. 3). After Libytheidae branched off, the female forelegs of the Nymphalid ancestor became small (the male forelegs became small earlier). The prothorax kept the sclerotized patagia of the butterfly ancestor, and the mesothorax anepisternum was present. The first stage larva kept the setae of the ancestor of all butterflies and skippers, except a few Satyrinae (*Cercyonis*), later lost one of the two SD setae on thorax segments 2-3, and first stage larvae later developed horns or tails or fleshy bumps or extra setae in some groups.

The first group to split from the Nymphalidae line was the ancestor of Danainae and Ithomiinae. (Waterhouse, 1953 also thought that Danainae branched off prior to Satyrinae and Nymphalidae because of its primitive type of adult peritrophic membrane.) Danainae-Ithomiinae obviously form a monophyletic group, and should best be lumped into one subfamily. Their ancestor developed fleshy filaments on the larva, except that *Anetia* of the Danainae and *Hymenitis* etc. of the Ithomiinae lack them today. Some species of both subfamilies now have only mesothorax filaments and have nearly identical larval color patterns (Young, 1981). Their ancestor developed a few secondary setae on the first stage larva, at least in *Danaus* (extra D setae) and (Müller, 1886) *Ithomia*. The males developed the unique habit of seeking a chemical (lycopsamine) from plants in order to make their male pheromones, which are distributed by hair pencils on the abdomen or wings (Edgar, 1975). Edgar thinks that the hostplant of their common ancestor (probably Apocynaceae, which some genera of both subfamilies eat today) had both lycopsamine for mating and cardenolides for poisoning predators (adults are models in mimicry), then the plants stopped producing lycopsamine to lessen larval feeding damage by forcing the adults to search for it elsewhere (adults must now obtain it from other plants such as heliotrope). Then most Ithomiinae switched to Solanaceae and most Danainae to Asclepiadaceae.

The mesothoracic anepisternum was lost in the Danainae-Ithomiinae ancestor, the meron developed a bulge above a caudal constriction, and the hypopteron became small. The anterior arms of the tentorium became small. This line then split into the ancestors of Danainae and Ithomiinae, and they then developed some peculiar traits, such as the scaleless antenna and abdomen hair pencils of Danainae, the fine dorsal tarsal spines (Forbes, 1939) and (often) dorsal hindwing hair pencils of Ithomiinae. Gilbert and Ehrlich (1970) note that adults of both subfamilies tend to feign death when handled (not a unique trait; I observed it frequently in *Poladryas minuta* and *Polygonia*, Nymphalinae, and it is recorded in *Nymphalis antiopa* and others).

Returning to the Nymphalid line, the larva developed two tails and two head horns, which most of the remaining Nymphalidae have (Ashizawa and Muroya, 1967 illustrate the tails and horns of Calinaginae). The adult peritrophic membrane now delaminated from the midgut epithelium (Waterhouse, 1953, though undetermined in Calinaginae). The anterior part of the adult midgut developed many processes (noted in Satyrinae, Apaturinae, and Nymphalinae by Homma, 1954; apparently absent in Danainae, Ehrlich and Davidson, 1961). Apparently the Calinaginae branched off next. Calinaginae seem to closely resemble what the ancestor of the remaining Nymphalids was like, although some derived characters are present (the gnathos is absent, and an extra uncus occurs above the usual uncus). The remaining Nymphalidae line then completely lost the claws on the female prothoracic legs (a weak trait, as claws occur in very few Nymphalids that split off earlier, namely Calinaginae and a few Ithomiinae which have small claws).

The ancestor of Satyrinae and Morphinae branched off next. The larvae of this ancestor began feeding on monocotyledons (although some, but not all, *Morpho* species later switched back to dicotyledons), and the adults probably developed many eyespots (which occur in most Satyrinae and Morphinae today), and developed a simplified toothed male valva. The line then forked, and the Satyrinae developed their swollen forewing veins, reduced hypopteron and anepisternum, and enlarged third larval eye, while the first stage Morphinae larvae grew a "fuzzy" head with hundreds of setae (forked at least in *Morpho*, Müller, 1886, and larvae raised and loaned by Allen Young) and added a few extra setae on the body (at least the hair-tufts present in *Morpho*).

The Brassolini have been placed in Satyrinae by Miller (1968), in Morphinae by Ehrlich (1958b). Some traits listed by Ehrlich support placing Brassolini into Morphinae (the hypopteron is well-developed, the mesothoracic anepisternum is larger, and the forewing veins are not swollen at the base). *Opsiphanes* (Brassolini) first-stage larvae have a fuzzy head (with hundreds of setae) (Casagrande, 1979; and photos by Allen Young) as do *Morpho* (Müller, 1886 illustrates single *Morpho* head setae, some multiply-split to the basal socket). The fuzzy head is so unusual (apparently unique) that I suggest it defines Morphinae (including Brassolini) as a monophyletic group. Morphinae also have a general propensity for communal larval feeding. Satyrinae clean the antenna by stepping on it while the antenna is pulled beneath the leg (Jander, 1966), which other subfamilies such as Morphinae may also do. Vane-Wright (1972) notes similarities of male abdominal hair pencils and egg shape between certain Biini ("Satyrinae") and Morphinae, so Biini may belong to Morphinae as well, though other characters should be examined also (abdominal hair pencils are also present in Danainae and such Nymphalinae as *Biblis*).

After the Satyrinae-Morphinae branch split off, the remaining line lost the veins closing the end of the discal cells. This character seems rather easily changed, as most Morphinae and some Satyrinae, both of which branched off prior to this point, have an open hindwing cell, and some descendants from the present ancestor regained a closed hindwing cell, namely Acraeinae and *Heliconius*, or a closed forewing cell, namely some Nymphalinae and Acraeinae. The male saccus may have lengthened (it is longer than the valva in European Charaxinae and Apaturinae). Young larvae developed the peculiar habit of silking dung pellets to a

leaf vein (known in Charaxinae, Apaturinae, Nymphalinae; Acraeinae probably have this habit, observations are needed). Then the Charaxinae branched off, and reacquired sclerotized parapattagia on the prothorax (one Nymphalinae genus also acquired them). The plump flanged pupa developed. Some first-stage Charaxinae larvae have secondary setae, horns and tails, but others lack these features. Some Charaxinae (*Hypna*, Young, 1982) have fleshy tubercles on older larvae, with a single spine on each tubercle of mature larvae, apparently independently evolved from the scoli of Nym.-Acra. (Acraeinae) which have many spines on each scoli.

The remaining Nymphalidae line then changed somewhat. The antenna may have become pendulum-shaped (except the clubs are more rodlike in *Limenitis*, *Doxocopa*, and others now), the anterior tentorium arms in the head started a thinning trend, and the mesothorax anepisternum disappeared.

Apaturinae split off at this point, and their larvae kept the two tails and two head horns of most Charaxinae, Morphinae, most Satyrinae, and Calinaginae, which branched off previously. Apaturinae have been treated as a tribe of Nymphalinae, as a subfamily of Nymphalidae, and even as a separate family. The adult traits are like those of Nymphalinae (Ehrlich, 1958b); however the larvae lack the branching spines of Nymphalinae. Other workers combine Apaturinae with the Charaxinae (which is untenable cladistically, violating the second principle of cladistics listed above, because Nymphalinae-Acraeinae is the sister-group of Apaturinae), but Ehrlich (1958b) found that the parapattagia on the adult prothorax are membranous, and there is no distinct anepisternum on the adult mesothorax, which distinguishes adults from adults of Charaxinae. The pupae differ greatly (Mosher, 1916), being flattened sideways except in the smaller species. The ancestral Apaturinae larva possibly ate *Celtis*. The larval and pupal traits warrant treating Apaturinae as a separate subfamily, related to Nymphalinae and to Charaxinae, and cladistic principle #2 requires this treatment. The main problem concerning Apaturinae is whether they are merely a minor branch (perhaps a tribe) of Nymphalinae which has lost the larval body spines of Nymphalinae. Of course all the genera with a spineless body could be placed in Apaturinae and the spined genera in Nymphalinae, but the correctness of such pigeonholing must depend on whether other characters produce the same subfamily assignments. The elongated cremaster of most *Asterocampa* is limited to a few genera of Apaturinae so does not help, but all Apaturinae have a particular arrangement of branches on the antlers of the larval head (T. Friedlander pers. comm.). Some Apaturinae genera (*Hestina*, *Sasakia*, etc.) have apparent paired "scoli" on the larval body, but T. Friedlander (pers. comm.) states that these are merely fused bases of chazae, a chazae being an integumental hill beneath a seta, and thus are probably not homologous with the true scoli of Nym.-Acra. and seem to represent incipient scoli.

The remaining line, after Apaturinae split off, then evolved branching spines (scoli) on the larval body (the head scoli perhaps required little modification from the horns of the Apaturinae ancestor), and the two larval tails were lost. The function of these tails has not been explained, but if we assume that they were used for camouflage, perhaps eliminating the shadow at the rear, or simulating leaf veins, they became useless as the larva's strategy shifted to conspicuous spines for armored defense. The male saccus apparently shortened. The ancestor then split

into two lines, Acraeinae and Nymphalinae, at this point. Both lines have a tendency to lose their arolium and pulvilli. Acraeinae have branching spines on the larval body (and often on the pupa), and other traits resemble those of Nymphalinae, except that they developed some peculiarities such as forked or asymmetrical leg claws. The pulvilli and arolium usually disappeared, the mesothorax anepisternum was lost, the anterior tentorial arms became thinner, the gnathos nearly disappeared, the abdomen elongated and the hindwing lost its abdominal flap, the female often developed a sphragis, and the discal cells on the wings became closed by cross veins.

Acraeinae is closely related to Nymphalinae cladistically (the larval scoli define Nym.-Acra. as a monophyletic group), and most genera of both subfamilies have only primary setae in first-stage larvae, but phenetically Acraeinae differs by an accumulation of these odd (mostly lost) traits. Acraeinae may actually not be a distinct subfamily; but just a side branch within Nymphalinae, perhaps near Heliconiini. Ehrlich (1958b) notes that Heliconiini falls in a continuum between Acraeinae and Argynnini, with the largest gap between Acraeinae and Heliconiini.

The remaining line is the Nymphalinae. I can draw no conclusions regarding the tribal evolution within this subfamily, except for the close relationship of Heliconiini and Argynnini. Such groups as Biblidini, Eurytelini, Limenitidini, Marpesiini, etc. (these names are properly spelled, J. Eliot pers. comm.) may not even be valid phenetically. The larva of *Marpesia petreus* is unusual, but that of *M. chiron* is like other Nymphalinae. *Limenitis arthemis* and relatives (and *L. ("Adelpha") isis* and *plesaure*, Müller, 1886) differ grossly in larva and pupa traits, but *L. ("Adelpha") bredowii* connects them to other Nymphalinae. A good generic classification is needed, including some new characters, such as the structures and habits of larvae and pupae.

The tribe Heliconiini of the Nymphalinae has often been elevated to family status, but probably evolved from a species similar to living *Euptoieta* but silver-spotted, the same species also producing the tribe Argynnini. This progenitor had androconial scales on the dorsal veins of fore- and hindwings of males, and the female had a dorsal scent gland between abdomen segments 7 and 8 used for mating. The male had a well-developed uncus (Emsley, 1963; dos Passos and Grey, 1945; the uncus is absent in Melitaeini at least in the European and American groups I am familiar with). Larvae lacked middorsal branching spines, and undoubtedly ate Passifloraceae and Turneraceae, which both tribes (*Euptoieta* among the Argynnini) eat today. In America there are two lines descended from this progenitor. The first line, Heliconiini, has humeral vein aimed toward the body, and, after *Dryadula* branched off, it evolved the female stink club on sternum 7 to repel males. This club swings up into the dorsal scent gland when not in use, and during mating fits into male valval glands (Emsley, 1963), where it picks up some chemical to activate the "stink" of mated females. The second line leading to Argynnini lost the branching spines on the larval head, and after *Euptoieta* branched off, females began to oviposit haphazardly near their hostplants, while first-stage larvae became the overwintering stage and developed extra (secondary) body setae. One can see the evolutionary progression in number of setae within Argynnini even today: *Boloria titania* has few secondary body setae, *B. eunomia* and *freija* have more, and *B. improba* and *Speyeria* have still more. Some species

of both tribes lost the silver spots. These two tribes are so similar that the wing veins of *Dione* (Heliconiini) and *Euptoieta* (Argynnini) are identical (except for the humeral vein): the five R veins branch from one stalk, a feature found in no other butterflies except the *Phyciodes frisia* group. Further, dos Passos and Grey (1945) note that *Euptoieta* is somewhat intermediate between the tribes in male genital structure. However, the picture in Asia differs (J. Eliot, pers. comm.). *Vindula* and *Cirrochroa* have the humeral vein forked (one branch proximal, the other distal), probably the condition in the progenitor of Heliconiini/Argynnini. *Vindula*, *Cethosia*, and *Terinos* have very long branching spines on the larval head, but the last two have a distally-directed humeral vein, although *Cethosia* (and *Vindula*) feed on Passifloraceae. Other Oriental "Argynnini" have branching head spines also. Evidently the tribes Heliconiini and Argynnini cannot be sustained on a worldwide basis, and the hostplant, humeral vein, and head spines are not consistent. Therefore, the two tribes probably should be combined into one, Heliconiini (by priority). Whether this combination is a monophyletic group remains to be determined. No doubt those Heliconiini with a stink club do represent a monophyletic group (perhaps including *Dryadula* which later lost it?). Certainly, elevating Heliconiini to family level is absolutely ludicrous.

Evolution of Libytheidae

Libytheidae evolved from ancestors which later produced Nymphalidae (Fig. 3), and the two families share many traits, such as antenna ridges. After the Nymphalidae ancestor branched, the first-stage larva developed a wide flange behind the head, and the second SD seta was lost on thorax segments 2-3. The palpi grew longer. On the prothorax, a muscle from the furca to the head rim became fan-shaped (prothorax character #9 of Ehrlich and Ehrlich, 1963), and the patagia became partly membranous. On the mesothorax, the preepimeron (Fig. 1) of Nymphalidae and Lycaenidae was modified (the function of the sulcus was taken over by thickening of the exoskeleton there; Ehrlich, 1958b draws a line illustrating this), the anepisternum was lost, and the postmedian wing lever (Fig. 1) became arrowhead-shaped. The mesothorax greatly overhangs the metathorax, which may provide more flight efficiency for migrations. A superuncus evolved on male abdomen segment 8. The mature larval prolegs have some crochets on the lateral side.

Evolution of Lycaenidae

Lycaenidae evolved from the butterfly line that also produced Nymphalidae and Libytheidae (Fig. 3). The Lycaenid ancestor was evidently small in size. The eyes stayed large for good vision while the head shrank, thus the eyes became notched (or at least the eye touches the antenna socket) after Styginae split off to allow room for the antennae, the frontogenal sulcus crowded against the eye, and the face became less arched. The labrum became small. The small size of the legs led to the pulvillae becoming single instead of forked.

The forelegs were obviously small in the lycaenid ancestor, because Jander (1966; see Fig. 15) found that Lycaenidae clean their eyes and antennae with the middle legs, even in living species (Polyommastini) with large forelegs, thereby suggesting that the forelegs were too small for cleaning when this behavior evolved. Special scale-brushes are on the middle leg for cleaning the antennae, a tuft of scales on the

femur opposed to an oblique trough-like scale brush on the tibia as noted by Eliot (1973) in nearly all Lycaeninae, and present in the same form in Riodininae in *Thisbe*, *Baeotis*, *Theope*, etc., and with the tibial brush reduced in many others. The femur brush at least was present in the ancestral species that gave rise to Lycaenidae, Nymphalidae, and Libytheidae, because all three clean the antenna with the middle legs, and the femur tuft is strong in Libytheidae and reduced or absent in Nymphalidae. The tibial brushes are absent or very weak in Nym.-Lib., though noticed by Ehrlich (1958a) in Danainae, so seem to have been well-developed only by Lycaenidae. Curetinae pupae have the middle leg touching the eye as in Nymphalidae (Shirozu and Yamamoto, 1957), which also suggests a small foreleg in the Lycaenid ancestor. The segmentation of the male foreleg of the Lycaenid ancestor is controversial, because today only the Styginae, a few Riodininae, some Miletini, all Liphyrini, very few Theclini, and Polyommattini have a segmented and clawed male foreleg tarsus (the "claw" just a single prong in Polyommattini), and the rest (including all Curetinae, Liptenini, Poritiini, Aphnaeini, and Lycaenini) have the tarsus reduced to one unclawed segment. It is traditional to assume that the segments and claws were independently lost many times. However, at least some Theclini seem to have reacquired segmented and clawed male forelegs (Eliot, 1973, pp. 394-395, perhaps by acquiring them using either mesothorax or female genes, females having fully formed forelegs. If genes for the segmented leg were on the Y chromosome, males could acquire the genes from crossing-over to an X chromosome (Eliot, 1973; as in Lepidoptera females are XY, males XX). The view that the Lycaenidae ancestor had only one unclawed tarsal segment on the male foreleg, and later lycaenids sometimes reacquired them, accords with the degenerate male foreleg of Libytheidae and Nymphalidae.

On the prothorax the patagia became membranous, and a muscle from the apodeme of the pronotum attached to the prescutum of the mesothorax much more to the side (prothorax character #7 of Ehrlich and Ehrlich, 1963). In the mesothorax the discrimen curved down to the base of the furca (apparently by using genes from the metathorax), and a muscle from the scutellum to the postnotum straightened (it was twisted; pterothorax character #7 of Ehrlich and Ehrlich, 1963). The male testis became white or yellow instead of red (Ehrlich, 1961). An elongate uncus is retained in Styginae, Riodininae, Curetinae, some Theclini and Polyommattini (J. Eliot pers. comm.), but the male uncus later became bilobed in many groups. A transtilla developed over the male valvae.

The pupa retained the silk girdle of the ancestor of butterflies and skippers (though it was later lost in many groups), and the pupal head has a tendency to become more ventral. Older larvae had a carpet of short setae, though the Liptenini-Poritiini and some Miletini and American Riodininae later developed long setae. The larval prolegs developed a unique fleshy lobe to help these small larvae stick to smooth surfaces such as fruits. The ventral neck gland was lost on the larva. The Lycaenidae ancestor probably ate plants, because carnivorous habits occur only in a few tribes of Lycaeninae, whereas plant-feeding is widespread. The lycaenid ancestor probably did not eat aphids (or other honeydew-producing bugs that are also tended by ants for honeydew), because this behavior is uncommon, and lycaenids that eat them today (Miletini) lack the honey glands and tentacles (Clark and Dickson, 1956) that were undoubtedly present in the lycaenid ancestor. The larvae became associated with ants, probably because the ancestor fed on flower buds and fruits and had to deal with ants that came to feed

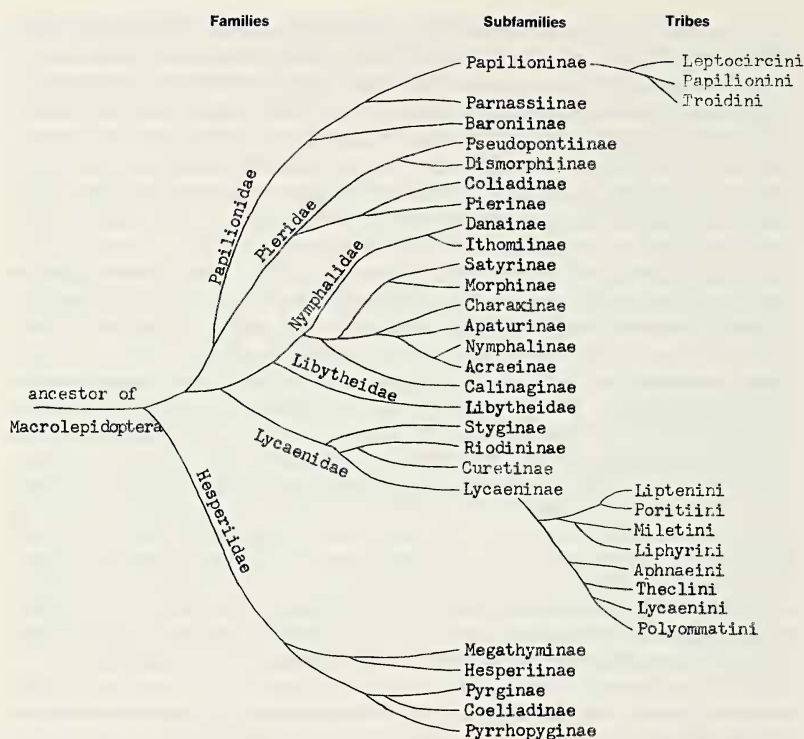


Fig. 3. Phylogeny accepted. The branching sequence represents inferred genealogy, whereas the sequence from top to bottom represents (as much as possible given the genealogy) the "distance" phenetic tree of Ehrlich, 1967.

on flower nectar (flower-fruit feeding would explain the small size of lycaenid adults also, because most plant fruits are small). At any rate, the association with ants caused the development of very thick skin to prevent damage from ant bites (Liphyrini and some Miletini later developed an even stronger armored skin), "performed cupolas" (microscopic glands that cause ants to touch the larva), honey glands (Newcomer's gland and "dew patches", that produce honey to bribe the ants), and eversible tentacles that apparently produce chemicals mimicking ant alarm pheromones to cause the ants to disperse (Malicky, 1970). These glands are present in both Riodininae and Lycaeninae. Riodininae have other glands called "vibratory papillae" on the prothorax (Ross, 1964). Curetinae possess eversible tentacles on very long pillars on abdomen segment 8, a tear-shaped supra-spiracular pit on each side of segment 8 that may be a honey-gland, and an odd translucent platelike organ (hollow beneath) above each spiracle on abdomen segment 7 (*Curetis acuta*, J. Scott, unpubl.). The association with ants also started a trend in larval shape, in which the head retracted into the thorax (except in Liptenini-Poritiini), probably to avoid ant attack (and the upper setae of the head shrank in order to fit the head into the prothorax). Ants began to tend lycaenid lar-

vae like cows, sometimes moving them about and even moving them into the ant nest. This allowed some lycaenid larvae to use ant larvae for food. The sudden drop of ripening fruits encouraged cannibalism (fallen larvae died, and the ones remaining on the plant had to cope with little food), which is frequent when lycaenid larvae are crowded. Fruit-feeders often cope with this by timing egg-laying on the flower buds so that most larvae mature before fruit-drop; in some cases the larva silks the fruit securely to the twig (J. Eliot, pers. comm.). Carnivorous habits led some Lycaenidae (Miletini, rarely others) to eat Aphididae and other plant-sap-sucking Homoptera as their only larval food. The hypostomal bridge on the larval head developed a unique wide gap. The first instar larva head generally nearly lost the F1 seta [lost in most Lycaenidae, present but extremely small in *Lycaena* first instars (Wright, 1983), and present in older larvae] which all other families have. The body developed chitin rings [= annuli = lenticles, apparently glandular structures (Wright, 1983), which may be related to perforated cupolas] and many extra setae including SV setae above the prolegs, and abdomen segments 9-10 generally became somewhat fused in appearance.

The first group to evolve from the lycaenid ancestor, most likely on the American side of Pangaea, was apparently the Styginae, which today is represented only by one large rounded-winged gray Andean species, *Styx infernalis*. Styginae retain various primitive characters, such as a large anepisternum, five radial veins, a wide face so that the eyes are not notched, a segmented and clawed male foretarsus (but the male foreleg is small, less than half the size of the middle leg), a humeral vein, tibial spurs, and a transtilla (the genitalia resemble those of Riodininae and Curetinae, J. Eliot, pers. comm.). In addition, Styginae are larger than most lycaenids, and there is a possibility that the larvae lack the ant adaptations such as thick skin and the various ant glands which may have evolved later. The Styginae also developed specialized traits, such as an ungrooved antenna, short palpi, the labial sclerite membranous in front of the palpi, short blunt tegulae, and two recurrent M veins in the forewing cell. One character, the very small male foreleg, suggests that Styginae arose from the base of the Riodininae line, and another, the ungrooved antenna, suggests that it arose from the base of the Lycaeninae line, but it seems best placed prior to both, certainly until its early stages are known.

After Styginae branched off, the lycaenid line then developed a slightly smaller anepisternum, characteristic of Riodininae and Curetinae, and the eyes became generally notched beside the antennae. The larva developed the ant-adaptations, if they were not developed earlier. The next to branch off was the Riodininae line. Eliot (1973) suggests that the ancestor of Riodininae and Lycaeninae existed before South America finally split from Africa in the Cretaceous, and then the Riodininae evolved mainly in America (only about 50 species are in the Old World), while the Lycaeninae evolved in the Old World. However, because Curetinae is Oriental, all three must have evolved before the split, and then each of the three survived only on one side of the split due to extinctions. Most American Lycaeninae belong to one group of Theclini which developed from perhaps only one ancestor that came into South America from Africa across the growing Atlantic Ocean (Eliot, 1973). Apparently *Brephidium*, *Leptotes*, and *Hemiargus* may have migrated or been blown from Africa to America in the late Tertiary, as they have not developed many American descendants, Eliot, 1973; *Feniseca* and *Zizula* also have few descendants and are related to African groups, or they may simply be old taxa that speciated little or most species died out. Some American lycaenids are

descended from ancestors that came across the Bering Strait from Asia (two Theclini, *Hypaurotis* and *Habrodais*, the Lycaenini, and most of the Polyommagini), and some American groups went the other way to Asia.

The Riodininae line evolved their characteristic spinelike projection of the male prothorax coxa below the trochanter. (The Curetinae probably branched off after this development, see below.) The male foreleg of Riodininae then became brushlike (with long scales), less than half the length of the middle legs, and the tarsus became reduced (rarely clawed, four-segmented to unsegmented today). The hindwing developed a short costal vein in addition to the humeral vein. Late instar larvae developed extra setae on the mandible (a dozen in *Apodemia*; some first-stage larvae such as *Apodemia*, and Curetinae and Lycaeninae and other butterfly and moth larvae have only two setae), "vibratory papillae" developed on the prothorax of some species (Ross, 1964) that pop out when ants are near. The typical positions of the ant-related glands changed in Riodininae or Lycaeninae, because they differ in the two groups. Newcomer's gland is on abdomen segment 8 in Riodininae and apparently in Curetinae, on segments 5-8 but usually on 7 in Lycaeninae. The eversible tentacles are on the metathorax and sometimes the rear in Riodininae, on abdomen segment 8 of Curetinae, on abdomen segment 7 in Lycaeninae. The Riodininae retained some primitive traits such as one groove on the antenna, an elongate uncus and a transtilla, plus tibial spurs.

In the Old World branch (Fig. 3) leading to Lycaeninae, the male foreleg stayed or grew a little larger (greater than $\frac{1}{2}$ the length of the other legs), and the antenna lost its groove. The late instar larva retained the two mandible setae of the lycaenid ancestor. The Curetinae doubtfully branched off at this point, if so, the male foreleg of the Lycaeninae ancestor lost the coxal extension past the trochanter that the Lycaeninae line must have had to produce this state in Curetinae. In the Lycaeninae line, now the anepisternum became small or absent, and the usual positions of the ant glands changed as noted above.

So far, two points of origin of Curetinae have been proposed, from the base of the Riodininae line, or the base of the Lycaeninae line (I agree with Shirozu and Yamamoto, 1957, that Curetinae is a distinct subfamily, phenetically between those subfamilies). A number of traits of Curetinae support its placement at the base of the Riodininae line: the male foreleg coxa extends below the trochanter nearly as far as in Riodininae, the male foretarsus is reduced (fused to a single unclawed segment), Newcomer's gland is on abdomen segment 8 in larvae of *Curetis acuta*, the anepisternum is fairly large (as in Riodininae), and the male genitalia are very similar (Shirozu and Yamamoto, 1957) with an elongate uncus and a true transtilla. However, some traits support its placement at the base of the Lycaeninae line: the antenna is ungrooved (an independent loss as in Styginae?), the older larval mandible has only two setae as two is the primitive state, and the male foreleg is larger than in Riodininae (this is probably the primitive state) and shaped as in many Lycaeninae with a tapered down-curved point. However, according to the leg theory of Eliot, 1973 and adopted in this paper, the Curetinae, Riodininae, and Lycaeninae independently evolved the fused clawless male foretarsus, so any similarity in shape is due to convergence. Most of these traits are primitive and thus unusable cladistically. Nevertheless, the extended male foreleg coxa is a derived trait perhaps unique in Lepidoptera, and definitely favors the Riodininae position. If this position is correct, principle #2 requires that Curetinae

be raised to subfamily rank. At any rate, Curetinae retained tibial spurs, but lost the humeral vein, and the antenna developed ventral bristles on the basal 3-4 segments. The middle leg of the pupa touches the eye as in Nymphalidae and Libytheidae (Shirozu and Yamamoto, 1957). The larvae eat green plants rather than other insects. The first-stage larval setae are mostly arranged as in some Lycaeninae. With the current state of knowledge, the large variation in setal patterns in Lycaenidae, especially in Riordininae, has defied analysis.

Returning to the Lycaeninae line, the true transtilla was lost, and then the Liptenini-Poritiini-Miletini-Liphyrini branch split off (Fig. 3). However a few members of this branch possess structures that are perhaps rudiments of a transtilla, so the last gasp of the transtilla may have been in the Lycaeninae line after this branch and prior to Aphnaeini. In any event, this branch lost the tibial spurs, and lost the larval honey glands, but retained the humeral vein. The Mil.-Lip. (Miletini-Liphyrini) stem then split off of this branch. Mil.-Lip. larvae are carnivorous, but generally eat different animals, Homoptera and ants respectively (except that *Aslauga* of the Liphyrini eats coccids farmed by ants, and some Miletini have been found in ant nests). The Liphyrini might be placed on the main Lycaeninae line prior to Aphnaeini, but the larvae of some Miletini (*Miletus*) have a tough leathery carapace which J. Eliot (pers. comm.) states is about intermediate between the extremes represented by *Thestor* (Miletini) and *Liphyra*. The characters that favor Liphyrini being placed on the main Lycaeninae line (larval tentacles, length of larval setae, humeral vein, transtilla?) are very weak, because most Miletini and Liphyrini genera are identical in these traits (see Eliot, 1973). Miletini larvae began to prey on Homoptera (Aphididae, Coccidae, Membracidae, Cicadellidae), and the larvae and adults of some (*Lachnocnema*, *Allotinus*, *Miletus*) even stroke these Homoptera to obtain honeydew. A "transtilla" is present in *Feniseca* and perhaps other Miletini, though whether it is homologous to the Styginae-Riordininae-Curetinae true transtilla is questionable. *Feniseca*, *Spalgis*, and *Taraka* developed some long larval setae, but other genera are short-haired and shaped as in other Lycaeninae. Some genera retained a segmented clawed male foreleg. The Liphyrini branch always retained segmented clawed male forelegs, but lost the humeral vein, and there is no trace of a transtilla. Their larvae apparently have cupolas, and *Aslauga* has tentacles. Larvae live in ant nests and have a leathery flange on the sides that droops to the ground to protect them from ants (larvae eat ant grubs). The pupae are attached only by the cremaster (or are inside the larval skin).

The Lipt.-Por. (Liptenini-Poritiini) line evolved a larva with a large non-retractable head and tufts of long setae, perhaps for protection against wasps and predators needed because of the loss of ant protection, although the larva of *Teratoneura*, Liptenini, has urticating dorsal setae on abdomen segments 1-4. The pupa became attached only by the cremaster, the male foreleg tarsus shrank to one unclawed segment, the saccus became aimed to the rear, and a sheath developed above the aedeagus (doubtfully a transtilla) that attaches to the bottom of the valvae. The line then split into two tribes, the African Liptenini whose larvae eat lichens and microscopic fungi (*Teratoneura* adults sip Coccid honeydew), and the SE Asian Poritiini whose larvae gregariously eat dicotyledon plants (the Poritiini developed ventral tufts of bristles on the abdomen tip, and spinelets instead of spurs on the end of the tibia).

Returning to the main *Lycaeninae* line, the transtilla was definitely lost at this point (if not earlier), the humeral vein disappeared, the proboscis lost nearly all of its setae, the hindwing probably developed tails, "hindwing rubbing" may have evolved, "dew patches" (honeydew glands) apparently developed on the larva, and the male foretarsus became a single unclawed segment (segments and claws were later regained by *Theclini* and *Polyommagini*). *Aphnaeini* branched off here. *Aphnaeini* were placed in *Theclini* by Eliot (1973), but I place them as a sister-group of *Theclini*-*Lycaenini*-*Polyommagini* because they have a cylindrical larva with a rather large non-retractable head, the male genital muscles differ from the latter three tribes (A. Sibatani, see Eliot, 1973, p. 470), five radial veins are retained from the lycaenid ancestor (as in *Liptenini*, some *Poritiini*, and *Liphyrini*), and the larval tentacles pop out of mounds as in some *Liphyrini*. Eliot (1973, p. 470) notes that the endodont of the tarsal claw is more prominent than in *Theclini*. This placement of *Aphnaeini* will be confirmed if adults are found to lack "hindwing rubbing"; the exact taxonomic distribution of this cladistically valuable trait must be determined. The *Aphnaeini* developed a few peculiarities also (a semi-membranous band connecting the two valvae in most genera, the leg claws are bifid, the underside generally has metallic spots). The larvae eat green plants (rarely ants).

The remaining *Lycaeninae* line lost one radial vein, and certainly (if not prior to *Aphnaeini*) developed "hindwing rubbing" to draw predators' attention to eye-spots and the antenna-like tail. At last the *Theclini* branched off, and some of these apparently regained a segmented clawed male foretarsus. Then the remaining line developed a flattened antenna club, and split into *Lycaenini* and *Polyommagini*.

There are insufficient good characters to be really confident of the tribal classification within *Lycaeninae*, as many characters represent losses of structures, and others are weak. The first stage larvae show such extreme variation that even they are not helpful at the present time. The presence or absence of a silk pupal girdle has not been used in this analysis because it seems a very weak trait (it is absent in all *Liptenini*, *Poritiini*, and *Liphyrini*, but present in some genera of all other tribes) because of its spotty occurrence in all groups.

Characters with Multiple Changes

An ideal cladistic classification is one in which each trait changes only once, and there are no reversals, parallel variation, or other complications. However, in most large taxa some characters do show parallel variation and reversals. It is worth examining these to make sure that the phylogenetic tree adopted is not incorrect.

The "lamella of the discrimen", a ridge in the bottom of the meso- and metathorax, is one such character. This discrimen curves downward to the base of the furca in the metathorax of all skippers and *Papilionoidea*, except *Pseudopontia* and to a slight extent in certain *Papilioninae*. The discrimen in the mesothorax curves downward to the furca in moths, skippers, and *Lycaenidae* (it curves down slightly in *Baronia* of the *Papilionidae*), but in the other *Papilionoidea* it runs straight back to the furca (Ehrlich, 1958b). The primitive state is for the discrimen to curve down to the furca base, as in moths and skippers, so one can hypothesize that it grew straight back in the mesothorax in the Pap.-Pier. line (perhaps twice, after *Baroniinae* evolved and in *Pieridae*) and in the Nym.-Lib. line. But it seems

more probable that the discrimen grew straight back in the mesothorax only once, in the Papilionoid ancestor (and in the metathorax of *Pseudopontia* the same thing occurred), and then in the Lycaenid ancestor (and slightly in *Baronia*) it curved down again, owing to the activation of metathorax genes.

The mesothorax anepisternum undergoes numerous changes, clearly independently. It is very large in moths and skippers, but became smaller in the Papilionoidea ancestor, and subsequently was frequently lost (by most Papilionidae, all Pieridae, the Danainae-Ithomiinae and Apaturinae-Nymphalinae-Acraeinae among the Nymphalidae, all Libytheidae, and most Lycaeninae of the Lycaenidae). The patagia has undergone many changes also. It is large in moths, skippers, Nymphalidae, and undoubtedly in the Papilionoidea ancestor, but was almost completely lost in Papilionidae and Libytheidae, in all Pieridae except Coliadinae, and lost in all Lycaenidae. This may represent as many as seven or more independent losses. The parapatagia seems to be another case of reversal. It is large and sclerotized in moths and skippers, but membranous in all Papilionoidea, except it has at least a trace of sclerotization in Charaxinae (and *Stibochiona* of Nymphalinae). It is much simpler to assume that this structure has become resclerotized in these two groups than to assume that it has been lost the eight or more times required by the hypothesis that Charaxinae retained it in an unbroken lineage from its moth ancestor. However, if the patagia could be lost numerous times, perhaps the parapatagia could be too.

The size of the male foreleg in the Lycaenidae seems rather conclusively to have reversed itself during evolution (Eliot, 1973; see Evolution of Lycaenidae). The ancestor of Lycaenidae (and Nym.-Lib.) probably had a five-segmented clawed male foretarsus, but it usually degenerated, and at least some Theclini later regained a larger segmented clawed male foreleg perhaps by using female (or pterothorax) genes. The arolium and pulvilli have also been lost independently (in Papilionidae, some Pieridae, some Nymphalidae (some Danainae and Nymphalinae, most Acraeinae)), and the pulvilli have become single in Pieridae and Lycaenidae. The claws often have become forked independently as well (in Pieridae, some Papilionidae, Nymphalidae (Acraeinae), Lycaenidae (Aphnaeini), and Hesperidae (*Epargyreus*)).

The wing veins have undergone many changes, including the well-known branching of the R veins. The R veins of Pieridae often became stalked from each other, independently (Klots, 1931) of similar evolution in Nymphalidae. The tiny CuP vein (the "Cu-V cross-vein" of Ehrlich, 1958b; Cu_1 and Cu_2 of most U.S. authors actually represent veins CuA_1 and CuA_2 , see Zeuner, 1943) present in Papilioninae (and as a rudiment in Heliconiini, etc. also) seems to be an advanced trait in adults. It is present in all Lepidoptera pupae, so is rather easily transferred to adults. A similar character is vein 1A+2A (commonly called vein 2A, see Zeuner, 1943). On the forewing these two veins usually join together at the base, forming one vein 1A+2A, but in Papilionidae they diverge. Because the veins are separate in the pupa, this is a simple derived feature.

"Secondary" setae (see Hinton, 1946) on first-stage larvae have developed independently several times, in Papilionidae, Lycaenidae, and in a few Nymphalidae (the Danainae, Morphinae, some Charaxinae; and some Nymphalinae, namely all Argynnini except *Euptoieta*).

Other characters with multiple changes are discussed by Ehrlich (1958b), and in

the "Origin of Pieridae" and "Origin of Lycaenidae" sections above. In general these are assumed to be due to parallel variation or reversal during evolution, as there is no way to arrange the butterfly family tree to eliminate problem characters.

Useless Characters

Some characters are very weak or useless. The "pilifers" on pupae (Mosher, 1916), which supposedly characterize Hesperioidea, Papilionoidea, Pyraloidea, etc., are not pilifers at all and should probably be called mandible remnants. True pilifers are tiny on adults, and absent in larvae, so one would not logically expect pupae to have large pilifers. Mosher's "gena" represents the orbit of the eye, often called the "smooth eyepiece." The secondary sclerite on the metascutellum cited by Brock (1971, p. 66) as present in Pieridae, Nymphalidae, and Lycaenidae, also seems useless. I examined all the families for this trait and could not find it in any, nor did Ehrlich (1958b). It is not demarcated by either a sulcus or a membranous area. Ehrlich (1960) and Miller (1971) list a "temporal suture" on the Hesperiid head, but, judging from the position of this sulcus, it is really the paratemporal sulcus, as suggested by Ehrlich (1960) himself, so there is no difference between skippers and Papilionoidea in this trait.

Several genital muscles studied by Stekol'nikov (1967) may provide useful characters when more complete studies are done: the "vaginal sclerite retractors and protractors" (= bursa dilators?), muscles to the membrane beneath the papilla analis, and the protractors of the aedeagus. Several generalizations made by Stekol'nikov are weakened by exceptions found by Arnold and Fischer (1977) and Ehrlich and Davidson (1961).

The "anterior sclerite" on the first abdominal sternite (sternum 2) was examined because Brock (1971, p. 66) suggested it might prove useful. I found much variation in it useful on the generic level, but probably not on the family level. In Hesperioidea this "anterior sclerite" is absent in *Epargyreus*, but an incomplete groove or small sulcus may indicate its presence in *Celaenorrhinus* (in which it is extremely wide, in front of diagonal scent pouches) and *Agathymus*. In Papilionoidea a groove or small sulcus may indicate its presence in Baroniinae, but it is absent in *Parnassius* and apparently in *Papilio*. In Pieridae (*Ascia*, *Phoebis*) a wide sulcus delimits it. In Nymphalidae it is delimited by a weak groove in *Anaea*, a stronger groove in *Danaus* and *Precis* (and the Libytheidae), a lateral groove leading to a medial membranous cleft in *Oeneis*, *Asterocampa*, and *Speyeria*. In the Lycaenidae a slight lateral sulcus delimits the anterior sclerite only laterally in *Eumaeus* (which also has a median-transverse cleft) and *Pseudolycaena*. The anterior ventral lamina of the metathorax furca (Brock, 1971) is absent or vestigial in all skippers and butterflies, though perhaps present in *Epargyreus*. The furcal stem shows very little difference in length among butterflies and skippers. Brock's postfurcal sclerite, which is a continuation of the epimeron forward and down toward the furcal foot, is rather variable, extending to the foot in *Epargyreus*, *Baronia*, *Parnassius*, *Papilio*, *Phoebis*, and *Precis*, extending about to the furcal stalk in *Libytheana* and *Eumaeus*, and is nearly absent in *Agathymus*, *Ascia*, *Anteos*, and *Pseudolycaena*. A little-noticed trait is the hairlike dorsal bristles just above the claws, which show some variation, but most groups seem to have six bristles.

Kristensen (1976, p. 31) implies that Dismorphiinae and Pseudopontiinae lack hind tibial spurs. However, the legs I examined show this character to be weak. The

tibial spurs are small in Dismorphiinae and some Pierinae, large in Coliadinae and some Pierinae. The trait would seem to be useful in generic classification, but is oddly not mentioned by Klots (1931). Kristensen also states that "the lateralmost tergal muscle between II and III" is absent in Dismorphiinae and Pseudopontiinae, and cites Ehrlich and Ehrlich (1963) as the source of this; however, I cannot find this character in the Ehrlichs' paper, and believe there must be some mistake.

Discussion

The evolutionary origin of the families presented as Figure 3 appears reasonable, because many robust derived traits support the monophyly of its branches. Another tree produced by intuitive analysis of adult morphology (Ehrlich, 1958b) is essentially the same except for a slight difference in the origin of Lycaenidae and a few differences within Nymphalidae (the positions of Charaxinae and Calinaginae were reversed there due to a misprint). A computer analysis of 196 external and internal morphological traits (the "distance" tree of Ehrlich, 1967) provided results compatible with the present tree (where two taxa join another line at nearly the same point in the distance tree, one cannot have confidence in their origin). Kristensen's (1976) cladistic analysis produced different results, but the present paper, based on the same cladistic methods but using a larger data set, shows Kristensen's conclusions regarding the origin of Pieridae and Libytheidae unwarranted.

One difficulty in the use of phenetic methods for the study of evolution of a group is that some groups change characteristics at a faster rate than do others. This confuses the phenogram such that the slowly-evolving taxa are grouped together, and the rapidly-evolving taxa are placed on their own branches. Among the butterflies, the Papilionidae and Lycaenidae may have evolved faster than other families (Ehrlich, 1958b notes that Papilionidae have a greater percentage of derived adult characters, and Lycaenidae certainly have the most derived characters of larvae, pupae, and eggs), so they have often been given exaggerated status in phenetic classifications (Ehrlich, 1967), being positioned farther down the trunk of the tree, while the Pieridae, Nymphalidae, and Libytheidae have been grouped together merely because they evolved slower. Also, the Pseudopontiinae among the Pieridae, and the Acraeinae among the Nymphalidae, have evolved many freakish traits (as if they have been through a "genetic bottleneck" of inbreeding in one very small population), which have exaggerated their status in the phenogram of their families as well. Nevertheless, phenetic classifications may be useful for special purposes, such as judging whether a monophyletic taxon (as determined by cladistic or genetic methods) should be treated as a family or subfamily.

Likewise, our knowledge of the phylogeny of the subfamilies of Papilionidae is sound, based on the work of Munroe (1961), Munroe and

Ehrlich (1960), Ehrlich (1958b), and Hancock (1983), although there is some uncertainty regarding the validity and origin of the tribes. Knowledge of the phylogeny of Pieridae subfamilies is sound also, thanks to Klots (1931), Ehrlich (1958b), and Geiger (1981), although a tribal classification has not been attempted.

However, the classification of Nymphalidae needs more study, as there is some controversy about the division between Satyrinae and Morphinae, and between Charaxinae-Apaturinae-Nymphalinae-Acraeinae, and the precise origin of Calinaginae is based on rather few characters. A search for new characters is needed in Nymphalidae, and some larval and behavioral traits need to be ascertained in some groups. The tribes of Nymphalinae need to be studied, because this is the most diverse subfamily. The results may affect the status of Acraeinae, Apaturinae, and perhaps Charaxinae. The Lycaenidae also need more study, as the relationship of the subfamilies and of several tribes of Lycaeninae is controversial. The tribes of Riodininae are also uncertain and the Hesperidae have certain problems. The relationship between the Hesperinae and Trapezitinae needs to be clarified, and the phylogenetic relationship between Pyrginae, Coeliadinae, and Pyrrhopyginae must be studied (it is possible that the latter two subfamilies are merely phenetically extreme offshoots of a polyphyletic Pyrginae). A tribal classification of Hesperidae is needed, as the current system seems weak.

Family vs. Subfamily Status.

Whether a subfamily is treated as a family or vice-versa is mainly a matter of philosophy, provided that principle #2, that each taxon must be monophyletic, is not violated. However, one can also use the degree of uncertainty of classification to help decide. For instance, the Riodininae and Lycaeninae (plus the Styginae) share numerous unique derived traits that distinguish them from other butterflies (see Lycaenidae) and there is no doubt whatsoever that they together form a monophyletic group, although they are sometimes treated as separate families. However, the subfamilies have a paucity of unique derived traits that would support their monophyly, and Eliot (1973, pp. 460-461) hinted that "all Riodininae may not be descended from one single ancestor and all Lycaenidae from another". The removal of Curetinae from Lycaeninae largely remedies this problem. Such uncertainty by an author of a higher classification of the Lycaenidae demands that we should treat these groups as subfamilies, because only the lumped family Lycaenidae promises stability.

A similar argument can be advanced for the family Nymphalidae, because the component subfamilies are a bit unsettled regarding how previous authors have treated their taxonomic affinity and their status. Thus the Ithomiinae have been considered close to Satyrinae (a treatment refuted by Gilbert and Ehrlich (1970)); some of the tribes included in Morphinae by Ehrlich (1958b) and the present paper were transferred to

Satyrinae by Miller (1968) while Vane-Wright (1972) transfers certain Satyrinae to Morphinae; the position of Calinaginae has been obscure; and the status of Apaturinae (as a member of Nymphalinae or even as a separate family) and its connection to Charaxinae has been shuffled about. Other Nymphalid taxa have been elevated to subfamilies or even families, such as Heliconiidae, "Marpesiinae", etc. Only the inclusive family Nymphalidae has had relative stability. While I am reasonably satisfied with the subfamily tree in Figure 3, there is a bit of a shortage of robust characters.

Actually the same argument could be advanced for treating Libytheidae as a subfamily of Nymphalidae, because Kristensen (1976) asserts that Libytheidae evolved from a Nymphalid, so must be a subfamily of Nymphalidae. However, the facts suggest that Libytheidae evolved from the Nymphalid root before the Nymphalidae evolved, so the treatment of Libytheidae is merely a matter of lumping or splitting.

The phenetic distance between subfamilies and families should also be used to define their family or subfamily rank. Probably because of the large number of species of Nymphalidae and Lycaenidae, these families have been divided into numerous weakly-defined "families." If splitting the families of Figure 3 is attempted, certainly the primary division of Hesperiidae would be one of the first to be recognized, as Pyrgidae and Hesperiidae. Baroniidae, Parnassiidae, and Papilionidae would have to be recognized, as well as Dismorphiidae, Pseudopontiidae, and Pieridae. Such splitting would then carve Stygidae from Lycaenidae, and Danaidae (including Ithomiinae) from Nymphalidae, but the Riodininae, Curetinae, Calinaginae, Satyrinae-Morphinae, Megathyminae, etc. would attain family rank only after a second round of splitting in which many subfamilies are raised to families. Such splitting seems rather pointless (who really cares whether a *d* replaces an *n* in the scientific name?), and Ehrlich is correct in attempting to make the butterfly families comparable to the families of beetles and microlepidoptera, even Noctuidae (which now contains the old families Notodontidae, Agariidae, Pericopidae, etc.), and to make family names comprehensive enough so that the average entomologist can recognize them. Indeed on various grounds it can be argued that Ithomiinae should be lumped into Danainae, Coeliadinae and perhaps Pyrrhopyginae lumped as subgroups of Pyrginae, Acraeinae lumped into Nymphalinae, and Libytheidae perhaps lumped as a subfamily of Nymphalidae.

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